40. The Mechanism of Suction in the Potato Capsid Bug, *Lygus pabulinus* Linn.

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(Text-figures 1–29.)

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Introduction.

The investigation of the mechanism of suction in *Lygus pabulinus* arose out of an inquiry by Professor Lefroy, of the Imperial College of Science, and Mr. Horne into the production by insects, on the foliage of the potato, of symptoms resembling those produced by fungi and by bacteria. They had produced definite symptoms by the infection of potato foliage with a Capsid (*Lygus*), a Jassid (*Eupteryx*), and other sucking insects; the symptoms were markedly characteristic of the different species; and the investigation of the actual mechanism of suction thus became necessary. I took up this inquiry at the suggestion of Professor Lefroy, who was in India at the time.

The insect is common on the potato and other plants during the summer. More than one species of *Lygus* is concerned with the damage to the plants. The species used in this investigation has been identified by Mr. W. L. Distant at the Natural History Museum as *Lygus pabulinus* Linn.

The scope of this paper is limited. It does not pretend to give full anatomical or morphological descriptions, but it describes the different structures of the head, both morphologically and anatomically, as far as they appear to be important in the mechanism of suction.

I very gratefully acknowledge my indebtedness to Prof. Lefroy for his help and encouragement during the whole of my work, to Mr. Clifford Dobell for his valuable criticism and suggestions, and to Mr. H. G. Newth for his assistance in preparing the paper for press.

* Communicated by Prof. H. Maxwell Lefroy, M.A., F.Z.S.

Material and Method.

I began my work in the Chelsea Physic Gardens of the Imperial College of Science, but, since the specimens were scarce, I had to go to Wisley, where I got good material through the kindness of Mr. F. Chittenden, the Director of the Wisley Horticultural Laboratory.

The following reagents were used for fixing the insects :—

(i.) Bouin's solution,
(ii.) Carnoy solution (Formula No. II),
(iii.) Petrunkevitch solution ;

and all of these have given satisfactory results.

The insects were kept in the fixing reagent for 24 hours, and, without being passed through the lower grades of alcohol, were thrown into 90 per cent. alcohol, in which they were allowed to remain for several weeks. Thus treated, they were sufficiently hardened for section-cutting, and it was, therefore, not necessary to keep them in absolute alcohol for more than three hours. After immersion for one hour in a mixture of equal parts of absolute alcohol and chloroform, they were transferred to pure chloroform, in which they were left for 24 to 36 hours. They were now imbedded in paraffin-wax (melting-point 56° C.) in the following way:—A saturated chloroform solution (in the cold) of wax of the same melting-point was prepared and the specimens were allowed to lie in it for two or three days at the temperature of the laboratory. They were then transferred to pure molten wax in the oven, where they remained for five hours. A block was then prepared in the usual way.

The importance of attention to the details of the above routine cannot be overrated. There is in the literature, so far as I can find, no single detailed description of a method by which good sections of hard insects can be got, and it is notoriously difficult to find any but diagrammatic illustrations to the papers of those who have investigated such forms. As the result, however, of my experiments, I have found that it is possible to obtain series of excellent sections, not only of *Lygus*, but of such hard and thickly-chitinised insects as the bed-bug, without using any reagent for softening the chitin. I am therefore justified in giving some prominence to the technique.

Long soaking in a mixture of chloroform and wax was found to be the only way to obtain proper impregnation, and the time given is the optimum—a shorter time is insufficient, a longer causes the tissues to become brittle. The length of the soaking differs with different insects, according to the quality of their chitin.

The sections were stained, in the ordinary way, with Ehrlich hæmatoxylin, orange G, and picric acid (saturated solution in 90 per cent. alcohol).

For macerating purposes, potash (10 per cent.) was used. A few drops of acetic acid were found useful. The specimens were generally cleared in turpineol, which did not make them brittle, even if they were kept in it for a long time.

Homologies of the Mouth-parts of Rhynchota.

The problem of the true homologies is very difficult, and has only recently been solved. In this section I propose to give a summary of the literature dealing with this problem.

Fabricius gave the name "Rhynchota" to the insects comprised in the class "Hemiptera," on account of their sucking mouth-parts. But till the time of Savigny (**42**), no attempt was made to homologise their mouth-parts with those of other (biting) insects. He hit upon the interpretation which is now generally accepted. According to him, the mouth-parts of the Rhynchota are homologous with those of the biting insects; the maxillæ, the mandibles, and the labium being represented in these forms by the internal stylets, the external stylets, and the proboscis, respectively. His interpretation has been endorsed by Kirby and Spence, Burmeister, and lately by Heymons and Leon.

Savigny and Cuvier, one with *Nepa cinerea*, and the other with *Ranatra linearis*, had found the labial palps articulated to the proboscis. But they could not discover any trace of the maxillary palps, which are well-developed structures in the biting insects. They had not, therefore, good evidence for the homologies of the maxillæ.

These matters will be better elucidated if the history of the homologies of each part be treated separately.

The Proboscis, or Schnabelscheide.

There were two views with regard to the structure of the proboscis before 1880:—

(i.) Burmeister (**5**), Latreille, and Graber held that the proboscis was formed by the second maxillæ fusing together with the labial palps. Burmeister has stated this view in very general and vague terms, but it was Kraepelin (**25**, **26**) who elaborated it in detail. According to him the first segment of the proboscis corresponds to the submentum and mentum together, and the three segments, 2, 3, 4, to the three segments of the labial palps of the biting insects. This view had been supported by the fact that there were, on the second joint of the proboscis, certain strong chitinous tubercles which were supposed by him to be the rudiments of the organs, *i. e.* extremities of external and internal lobes of the palps. Leon (**30**), however, takes them to be the chitinous supports for the muscles of the proboscis, running into the head.

This view has been exploded, and no present-day writers think seriously of it, its interest being now purely historical.

(ii.) The second view was first formulated by Savigny and Cuvier, and is now generally accepted. Savigny, in *Nepa cinerea*, and Cuvier, in *Ranatra linearis*, discovered certain jointed structures articulated to the proboscis, which they took to be the labial palps. The palps are, therefore, in this view, separate from the proboscis, and do not take any part in its formation, the proboscis being formed by the fusion of the second maxillæ only.

After Savigny comes Gerstfeldt (**14**). He elaborated this view as Kraepelin had done the earlier one. According to him:

"Das erste Glied das nach Burmeister allein die Unterlippe darstellt, wäre an das submentum und entspräche den Cardines der Lippenkiefer, das zweite Glied bestände aus den beiden Stipites und wäre analog dem Mentum, das dritte und vierte Glieder gehörten zusammen den Endlappen der Unterlippe an und entsprachen entweder nur den ausseren Laden (Paraglossæ) oder nur den unteren Laden (Ligulæ), oder aber, was mir noch wahrscheinlicher ist, beiden mit einander vereinigten Ladenpaaren zugleich."

Leon (**29–33**) has fully dealt with the question of the homologies of the proboscis. His examples are taken from the Belostomidæ. He clearly demonstrated the presence of the labial palps as distinct from the proboscis, and came to the following conclusion, after examining all the examples:

"Es ist ganz gleichgültig, in welcher Weise die Glieder der Scheide von einer Art zur andern, sei es als Form, Grosse, als Borstenanzahl, als Chitinerhebungen, etc. variieren möchten, eins bleibt immer constant, das die Scheide aus derselben Zahl von Gliedern besteht, die immer dieselbe Stellung zu einander haben und die vollkommen homolog sind den Bildungsgliedern des Labiums der beissenden Insecten."

In the meantime, Dr. R. Heymons (**18**) had published the result of his study of the development of certain rhynchotous forms. His conclusions are:—(1) the labial palps have entirely disappeared in the adult Rhynchota; (2) the so-called labial palps are secondary structures from the third segment of the proboscis; they appear in the embryo but they degenerate and disappear in the later stages. Leon, however, does not agree with these conclusions. Heymons has deduced them from the study of the comparative embryology of these forms; while Leon has come to his different conclusions from the study of their comparative anatomy. His conclusions are:—(1) The labial palps persist in the adult forms; (2) they have been discovered in *Nepa*, *Ranatra*, and certain Belostomidæ; (3) it is not possible for any secondary structures to originate at the same place where the primary structures had been before, and to perform the same function as the latter.

While the homologies of the labium were being discussed in Europe, a novel interpretation of the same structures was put forward in America by Prof. J. B. Smith (**45**), who had brought his special knowledge of the mouth-parts of Diptera to bear upon this question. He held that the proboscis was a part of the first maxillæ; the basal segment of the proboscis being the cardo; the second, subgalea; the third and the fourth, the two segments of the galea. All that remained of the labium was the mentum—a boat-shaped process lying between the stylets. This was an original view, confined to Smith alone. It was shown, the next year, to be erroneous by Marlatt (**34**), and, after a few years, by Meek (**36**), according to whom the boat-shaped process—the mentum of Smith—was the pharynx.

Thus far no one has definitely demonstrated the presence or absence of the labial palps. All the recent writers are unanimous in the view that the proboscis is formed by the fusion of the second maxillæ, which consist of the submentum, mentum, paraglossæ, and ligulæ—the view held by Gerstfeldt long ago. But here unanimity ends, and different views prevail as to the existence of the labial palps.

(i.) Leon holds that they are present in the adult forms. He deals with this question from the anatomical standpoint.

(ii.) Heymons holds that the labial palps appear only in the embryonic stages, and disappear in the adult forms. He writes: "Wenn einigen Autoren auch gewisse Anhänge an der Unterlippe, also Palpi labiales angesprochen worden sind, so wird man sich diese Deutungen gegenüber skeptisch verhalten müssen, da weder die Entwickelungsgeschichte, noch die vergleichende Anatomie zu Gunsten solcher Ausnahmen sprechen."

Maxillæ, or inner Borstenkiefer, or Stechborsten.

Savigny long ago, and others who have followed him, have homologised the inner stylets of the Rhynchota with the first maxillæ of the biting insects. But they have not clearly shown what parts correspond to cardo, stipes, etc., and what becomes of the maxillary palps—which are conspicuously absent in the Hemiptera.

Kraepelin (**25**) held that the grooved inner stylets were mandibles, which formed the tube for suction, while the maxillæ were on the outside of the mandibles. This view is not now accepted.

Huxley (**48**) denied the homologies of the inner stylets with the first maxillæ of the other (biting) insects, because the former do not happen to possess the maxillary palps of the latter.

Mecznikow (**49**) has also denied the homologies of the internal and the external stylets in the Homoptera. According to him the true maxillæ and mandibles appear in the embryonic stages only, but they degenerate and disappear later on. Both stylets of the adults are produced from the retort-shaped ("retortenformigen") organs situated in the head. They are therefore not homologous with the maxillæ and the mandibles of the biting insects.

Witlaczil (**50**) has demonstrated, however, that the embryonic mandibles and maxillæ do not disappear at all, but persist in the adult stages, though there is a marked change in their position. In early stages they are situated on the outside, but later on they sink into the head and become entirely internal.

This sinking in, or involution, of these structures has been brought about by the greater development (overgrowth) of the clypeus and the labrum. The retort-shaped organs are nothing but the swollen bases of these stylets. Not only are these organs found in the Homoptera but they are also found in the Heteroptera; though in the latter they are not so prominent as in the former, owing to their degeneration. In the Homoptera they have been recently demonstrated by Davidson (9).

The fact that both the stylets sink into the head owing to the overgrowth of the clypeus, has been recently shown by Heymons.

The mandibles and the maxillæ, then, do not disappear but persist in the later stages, though in different positions. "Mandiblen und Maxillenladen ziehen sich bei den Rhynchoten in tiefe taschenformigen Hohlungen zuruck und scheiden die chitinosen Stechborsten aus." Thus writes Heymons. The retort-shaped organs of Mecznikow, in the Homoptera, are the "taschenformigen Hohlungen" of Heymons, in the Hemiptera in general.

Prof. J. B. Smith (45) was the first to call attention to the fact that the maxillary stylets form but a part of the first maxillæ. Each maxilla consists of two parts: the maxillary sclerite or segment, and the maxillary stylet; but he was not able to identify them separately.

It was not until Heymons had published his "Beiträge zur Morphologie und Entwickelungsgeschichte der Rhynchoten" (20), that the relation between the maxillary segment or plate and the maxillary stylet was clearly understood. According to Smith the two pairs of stylets with the lateral (maxillary) sclerites posterior to the mandibles, together with the proboscis, represent the first maxillæ; the stylets representing the lacinia and stipes; the sclerite representing the palpus and the proboscis. He had made both the stylets arise from the same place. He is apparently led astray in his interpretation by a faulty dissection, which was shown to be the case by Marlatt (34).

Heymons is the first writer to explain clearly the homologies of the first maxillæ. He has studied their development in certain Hemipterous (both Heteropterous and Homopterous) forms. He has clearly demonstrated that a maxilla arises as a single structure, but that soon after it is divided into two parts:—(i.) a median piece, or maxillenlade; (ii.) a lateral piece, maxillenhöcker, or maxillary plate (segment).

(i.) *The maxillenlade.*—This becomes elongated and transformed into a long tapering stylet, two of which (one from either side) combine together to form two tubes, one for suction of the sap, and the other for ejection of the saliva.

(ii.) *The maxillary plate.*—This represents the stem of the maxilla (cardo and stipes) of the biting insects. It forms the antero-lateral piece of the head-wall, and has therefore nothing to do with the mouth-parts proper—except in so far as it forms the support to the protractor muscles of the maxillæ.

The Maxillary Palps.

The presence of maxillary palps is one of the distinguishing features of the first maxillæ of the biting insects, but they have completely disappeared in the Rhynchota. The maxillæ become elongated in these insects, and work inside plant or animal tissues. Sensory apparatus in the form of palps is superfluous.

Maxillary palps had been described long ago by Ratzeburg (1827–34) in certain species. Each palp was found to be three-jointed. Burmeister (1835) had, however, found that they were not palps but horny tubercles marking the attachment of the maxillary muscles.

Heymons has, as far as possible, elucidated the question of the maxillary palps. According to Smith, the maxillary sclerite and the palps fused together to form one structure. Heymons, however, holds another view. The maxillary palp is distinct from the sclerite, and the maxillary plate has a process (processus maxillaris) which he interprets to be the remains of a maxillary palp. In some species of Tingidæ there are certain processes—which were taken to represent the labial palps—but which are now regarded as the maxillary palps.

Rudimentary palps are present in some Hydrocoridæ—in *Nepa* they are onion-shaped—but in Gymnocerata they are identified with the Bucculæ (?).

Mandibles, or external Stechborsten.

These were recognised as such long ago, though Kraepelin (**25**) had mistaken them for the maxillæ, and had therefore made them the sucking organs. The views of Mecznikow have been given above. Prof. Smith, while working on the nymph of *Cicada*, described a mandibular sclerite corresponding to that of the maxilla, and a mandibular stylet also corresponding to the maxillary. Heymons, too, has described the mandibular sclerite (lamina mandibularis) and stylet in *Cicada*. The mandibular sclerite is very well marked in the Homoptera, but in the Heteroptera it is not present at all, or is rudimentary. These structures are distinct in the later stages, though they have been derived from the same structure in the embryo; the connection between them is lost. The protractors of the mandibular stylets are not attached to the mandibles but to their levers at one end and, at the other, to the mandibular sclerite.

This interpretation of Heymons has been recently called in question by Muir and Kershaw (**22**, **23**, **24**). The so-called mandibular plates are not derived, according to them, from the mandibles, and therefore have no relation whatever to them. They are mandibular folds or sulci.

The most recent view therefore is :—(i.) The mandibles of the biting insects are represented by the external stylets. (ii.) The mandibles are not divided into two parts, one corresponding to the cardo and stipes of the maxillæ and the other to the maxillary stylet. (iii.) The protractor muscles of the mandibles are attached to the levers and not to the mandibles.

Labrum.

This is the least disputed structure. Its homology with the labrum of the mandibulate insects has been determined with certainty. It is not, however, one of the appendages of the head but a continuation of the clypeal sclerite, from which it is not easily to be distinguished externally.

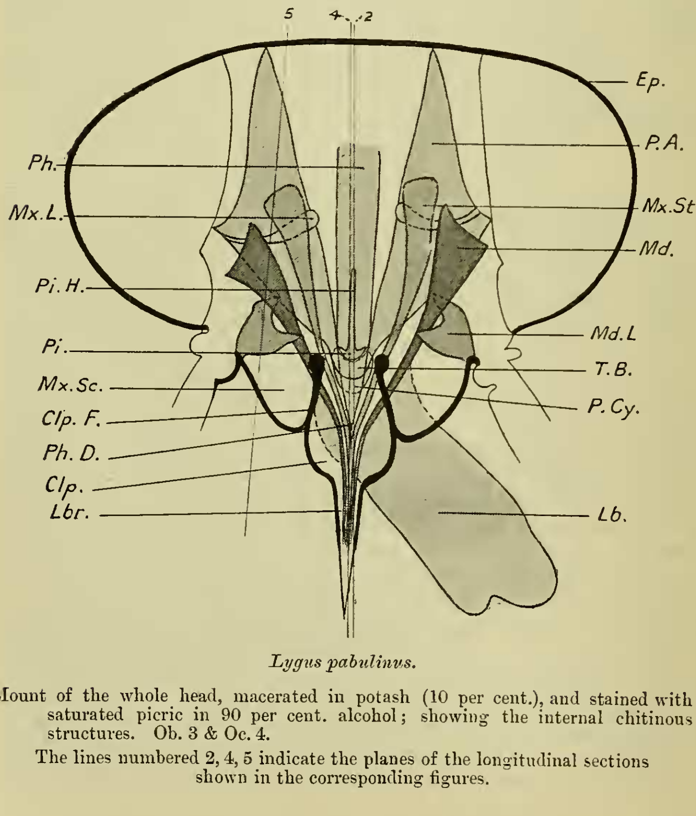
THE MORPHOLOGY OF THE HEAD. (Text-fig. 1.)

The head of *Lygus pabulinus* consists of the following parts:—

(1) *The Epicranium.*—This lies between the two large eyes. It is continued into

(2) The *Clypeus*. (The frons, the intermediate portion between

Text-figure 1.



Lygus pabulinus.

Mount of the whole head, macerated in potash (10 per cent.), and stained with saturated picric in 90 per cent. alcohol; showing the internal chitinous structures. Ob. 3 & Oc. 4.

The lines numbered 2, 4, 5 indicate the planes of the longitudinal sections shown in the corresponding figures.

epicranium and clypeus, is not well marked.) The sides of the clypeus have sunk into the head, forming clypeal folds to which the protractors of the mandibles are attached, and which are fused with the ventral wall of the pharynx (text-fig. 17, Clp.F.).

(3) *The Labrum.*—This is merely a continuation of the clypeus, and there is no sign of external differentiation between the two structures. It extends as far as the first segment of the labium, and tapers to a point, the base being broader. It has rather a deep groove underneath to hold the stylets in place, since the labial groove at this point is too shallow and flat to do this. There are three external longitudinal ridges on its dorsal surface; its sides are ornamented with small rounded lobes, and its surface

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Explanation of Lettering.

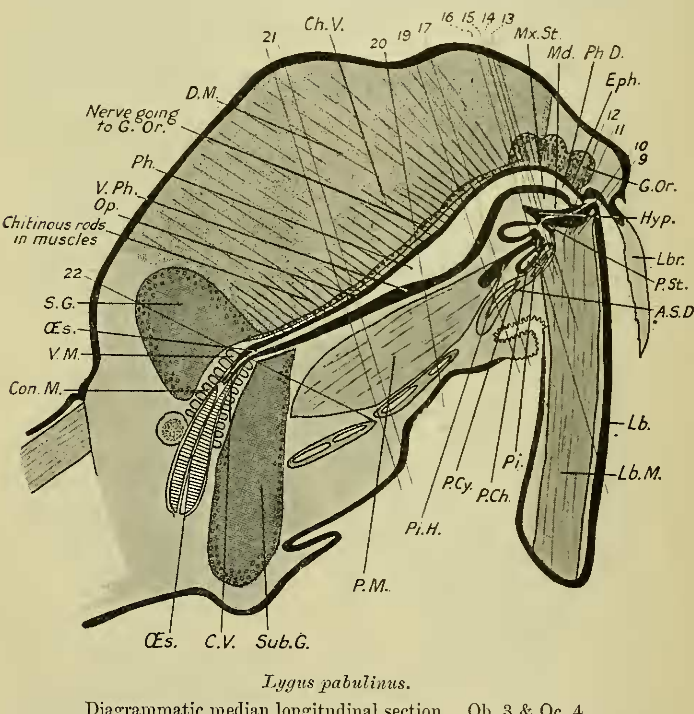
A.M. Antagonistic Muscles.
A.S.D. Afferent Salivary Duct.
A.W.P. Anterior Wall of the Pump-chamber.
Bu.F. Buccal Fold.
Cam. Cambium.
C.C. Circumœsophageal Commissure.
Clp. Clypeo-labrum.
Clp.Lbr. Clypeo-labrum.
Clp.F. Clypeal Fold.
Clp.Sc. Clypeal Sclerite.
Con.M. Constrictor Muscles.
Cort. Cortex.
Cri.Pl. Cribriform Plate.
C.V. Cardiac Valve.
D.A. Dorsal Arms of the Tentorium.
D.M. Divaricator Muscles.
E.C. Ejection Canal.
Ep. Epicranium.
Epd. Epidermis.
Eph. Epipharynx.
End. Endodermis.
E.S.D. Efferent Salivary Duct.
G.Or. Gustatory Organs.
Hyp. Hypopharynx.
L.A.S.D. Lumen of the A.S.D.
Lb. Labium.
Lb.G. Labial Groove.
Lb.M. Labial Muscles.
Lbr. Labrum.
Lig.A.M. Ligament for A.M.
Lig. Ligament for D.M.
L.P.M. Ligament for P.M.
Md. Mandibles.
Md.Art. Mandibular Articulation.
Md.L. Mandibular Lever.
Md.P. Protractors of the Mandibles.
Md.R. Retractors of the Mandibles.
Md.C. Cavity of the Mandibles.
Md.H. Hooks of the Mandibles.
Md.Sh. Mandibular Sheath.
M.A.S.D. Mouth of the A.S.D.
Mx.C. Cavity of the Maxillary Stylet.
Mx.F. Maxillary Fold.
Mx.L. Maxillary Lever.
Mx.P. Protractors of the Maxillary Stylets.
Mx.R. Retractors of the Maxillary Stylets.
Mx.Md.Art. Maxillo-mandibular Articulation.
Mx.Md.M. Maxillo-mandibular Muscles.
Mx.Sc. Maxillary Sclerite.
Mx.Sh. Maxillary Sheaths.
Mx.St. Maxillary Stylets.
Op. Operculum.
Œs. Œsophagus.
P.A. Posterior Arms of the Tentorium.
P.Cy. Pump-cylinder.
P.Ch. Pump-chamber.
Pi. Piston.
Pi.H. Handle of the Piston.
Ph.D. Pharyngeal Duct.
Ph. Pharynx proper.
Phl. Phloem.
P.M. Pump Muscles.
Poc.Or. Retort-shaped Organs.
P.St. Pump-stem.
P.W.P. Posterior Wall of the Pump-chamber.
S.St. Maxillary Process or Supporting Strut.
Su.C. Suction Canal.
S.G. Supra-œsophageal Ganglion.
Sub.G. Sub-œsophageal Ganglion.
S.D. Salivary Duct.
T.B. Body of the Tentorium.
Tr. Trachea.
T.Mx. Tip of the Maxillary Stylet.
T.Md. Tip of the Mandible.
V.Ph. "V" or ventral wall of the Pharynx.
V.M. Valvular muscles.
Xyl. Xylem.

is covered dorsally with small hairs or papillæ, and is very smooth ventrally. It is complementary in its function to the labium, *i. e.* it is applied closely against the labium to form the deep groove which keeps the stylets in place and prevents their lateral movement (text-fig. 9, Lbr.).

(4) *The Maxillary Sclerite.*—This is situated laterally to the epicranium just below the eyes, and forms the lateral boundary of the mouth. As stated above, it is one of the parts of the embryonic maxilla. The protractors of the maxillæ are attached to it.

(5) *The Labium* (text-figs. 1, 29, Lb.).—This structure consists of four segments. The first is broader and shorter and has practically no groove, or, if there is any, it is very shallow and flat. The first joint—*i. e.* the joint between the first and second segments—is swollen, and this swelling is due to a great development of chitinous "tendons" to which the labial muscles are

Text-figure 2.



Lygus pabulinus.

Diagrammatic median longitudinal section. Ob. 3 & Oc. 4.

The lines numbered 9 to 22 indicate the levels of the sections shown in the corresponding figures.

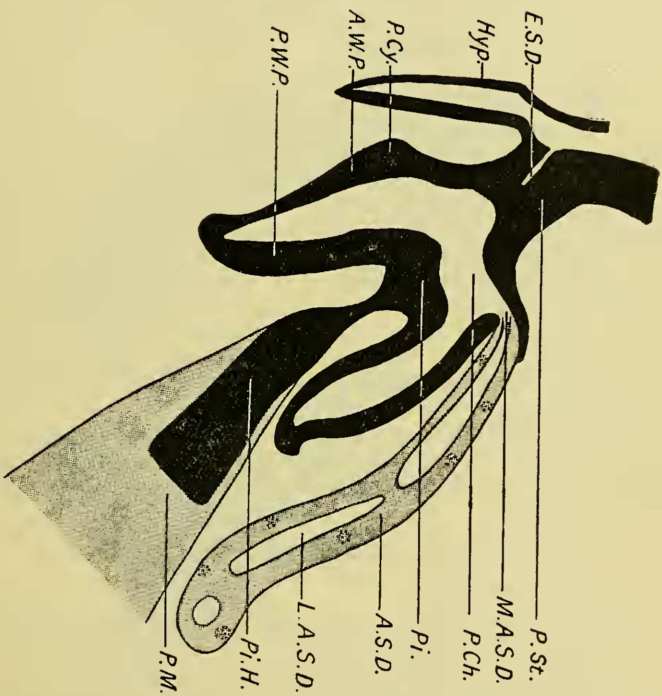
N.B.—In all the sections the microscope tube is not drawn out to its proper length.

For explanation of the lettering see p. 693.

attached (text-figs. 2, 16, Lb.M.). Moreover, it acts as a hinge upon which the whole of the labium is bent and doubled. This is one of the characteristic features of the insect. In enables the insect to get at the required tissues of a plant. The stylets are thrust into tissues containing food, the depth of which below the surface varies in different parts of the same plant. The deeper such tissue lies, the greater is the bend of the labium at the first joint. Its bend is scarcely appreciable when the insect is sucking sap from tissues which are superficial.

The stylets cannot be increased in length, but this mechanism by shortening the proboscis enables the insect artificially to protrude them further into the plant tissue. The labial muscles facilitate this bending (text-figs. 2, 16, Lb.M.).

Text-figure 3.



Pump-apparatus of *Lygus pabulinus*.

Sagittal section.

For explanation of the lettering see p. 693.

The second, the third, and the fourth segments are long and narrow and gradually taper to a point. The groove, which is shallow and flat in the first segment, begins to deepen in the second, and, in the last segment, forms a tube enclosing the stylets. Cross-sections of the last segment show one tube within the other. The inner tube enclosing the stylets is formed by the groove; and the labium is the outer tube which encloses the former (text-fig. 8, Lb.G.).

The tip of the labium is encircled with bristles which are of two sorts, fine and stiff. They are arranged in a definite way, and function as sensory hairs. The insect feels the surface of a leaf with them before thrusting its stylets into it.

The labrum and the labium together keep the stylets in place. In the first segment, where the labial groove is too flat and shallow to do it and where the labium has a bend inwards, thereby leaving the stylets free, the labrum encloses them in its groove. Distally the labium takes over this function of holding the stylets, since its groove becomes deeper and deeper. Thus the stylets are always found in the groove of one or the other, and are prevented from that lateral movement which would make piercing and sucking impossible.

The labium protects the stylets in the groove, but its more important function is very ingenious. The stylets are very thin, needle-like structures which have, however, to pierce the tough and cuticularised epidermis of a leaf. As they are very delicate, they would bend in the act of piercing, were they not enclosed in the proboscis. The lumen of the tubular tip of the proboscis is so small that the stylets fit into it tightly (text-fig. 8). There is no empty space in it for them to bend. The tip of the labium is closely applied to the surface of the leaf; the protractor muscles of the stylets contract; and the stylets are forced out of the proboscis and driven against the epidermis, which they cannot fail to pierce. Once in, their forward progress to the required tissue is mechanical owing to the bend of the labium at the first joint.

It is thus obvious that the labium is an important structure in the sucking apparatus of this insect; it is one, moreover, on the structure of which stress has not been laid by previous writers.

(6) *The Stylets, or Stechborsten.* (Text-figs. 1, 6, 23.)

(I) Morphology.

(*a*) The Maxillary Stylets or Internal Stechborsten. (Text-figs. 1, 5, 6, 23, Mx.St.)

It is shown above that the stylet is a part of the maxilla and not the maxilla itself. Each maxilla is divided, in the embryonic stage, into two parts, one of which forms the stylet or Stechborste. The maxillary stylets are situated between the pharynx and the mandibles on either side. They are not, however, on the same level with either of them: they are just above the pharynx and below the mandibles. They are hollow, and their cavities are continuous with the body-cavity.

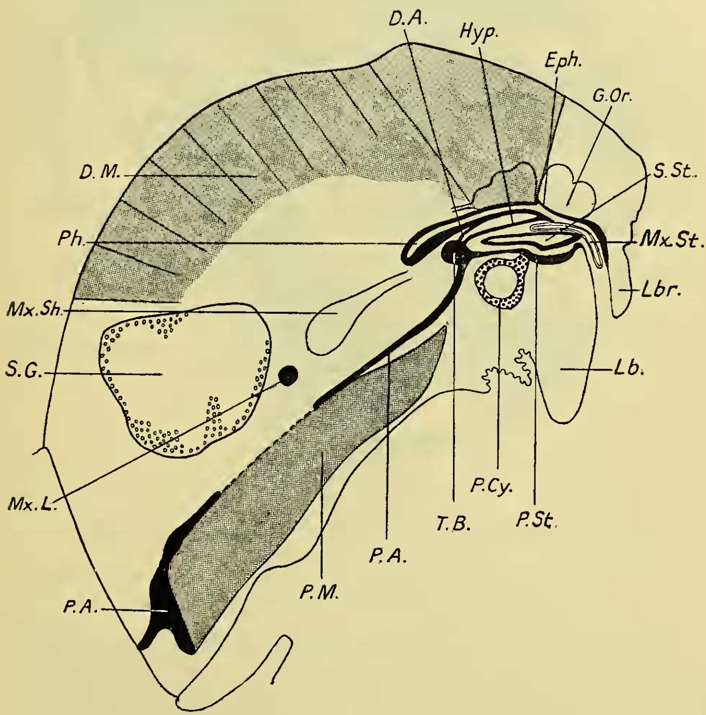
Each of them consists of :—

(i.) an external part, projecting beyond the head and forming the complementary half of the sucking tube ;

(ii.) an internal part, separate from its complement and going to one side of the pharynx.

(i.) The external part. This tapers to a fine and curved point. In cross-sections it shows a groove which is divided into two gutters by a longitudinal ridge which runs through it, from end to end. In short, the whole structure looks in cross-section like a **W**, and one groove is thus divided into two small, separate, and non-intercommunicating groovelets. The two stylets from either side come together and by approximation of these groovelets form two complete tubes—one dorsal facing the labrum and functioning

Text-figure 4.



Lygus pabulinus.

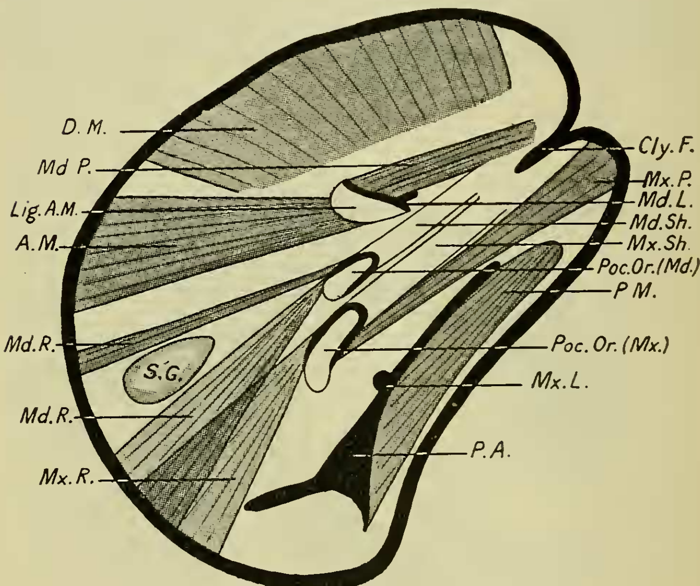
Nearly median longitudinal section, showing the supporting structure, the body of the tentorium, the pump muscles, etc. Ob. 3 & Oc. 4.

For explanation of the lettering see p. 693.

as the suction-canal, and one ventral facing the labium, functioning as the ejection-canal, through which saliva is forced down by the salivary pump (text-figs. 8, 9, 10, Mx.St., Su.C., E.C.).

There are not any extra-chitinous structures to unite the two stylets to form the canals; the three ridges of each stylet apparently uniting with those of the other. They can be detached from one another with a little force. This fusion may easily be seen in a series of cross-sections.

Text-figure 5.



Lygus pabulinus.

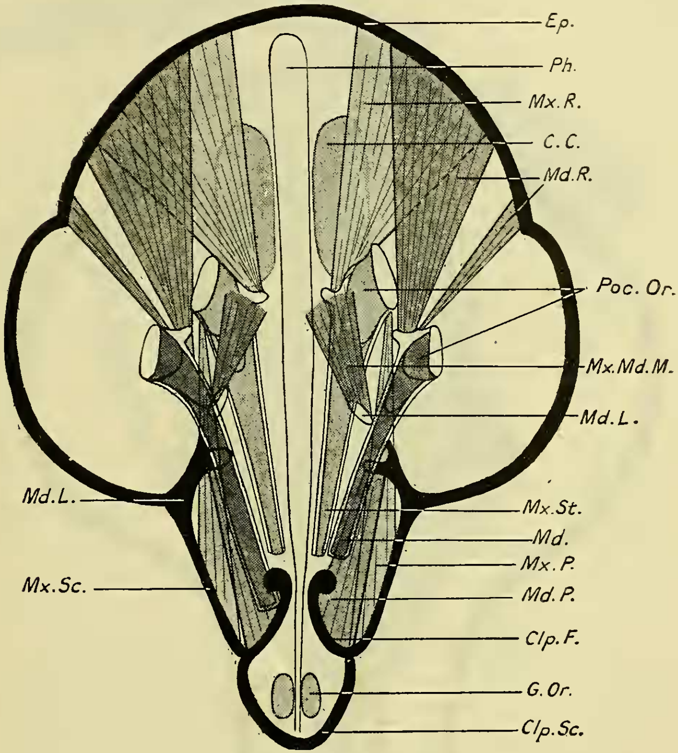
Lateral longitudinal section, showing the arrangement of the muscles in the head. Ob. 3 & Oc. 4.

For explanation of the lettering see p. 693.

The tips of the stylets are smooth and lancet-shaped, as might be expected from their function (text-fig. 23). In certain aquatic forms they are ornamented with minute incurved hooks (O. Geisse (**13**). Within the plant-tissues the tips of the maxillæ do not end simultaneously; one of them is pushed a little further than the other (text-fig. 25).

(ii.) The internal part. This lies within the head. It gets gradually flatter and broader when it is traced back. Each stylet ends internally in a swollen base. These swollen bases, which are oval, have their importance in history, which has been referred to above. They are known as the retort-shaped organs of Mecznikow, or the Taschen-formigen organs of Heymons (text-figs. 5, 6, 20, 21, Poc.Or.).

Text-figure 6.



Lygus pabulinus.

Reconstructed from numerous vertical sections, showing the relation of the muscles to the stylets, the pump, etc. Ob. 3 & Oc. 4.

For explanation of the lettering see p. 693.

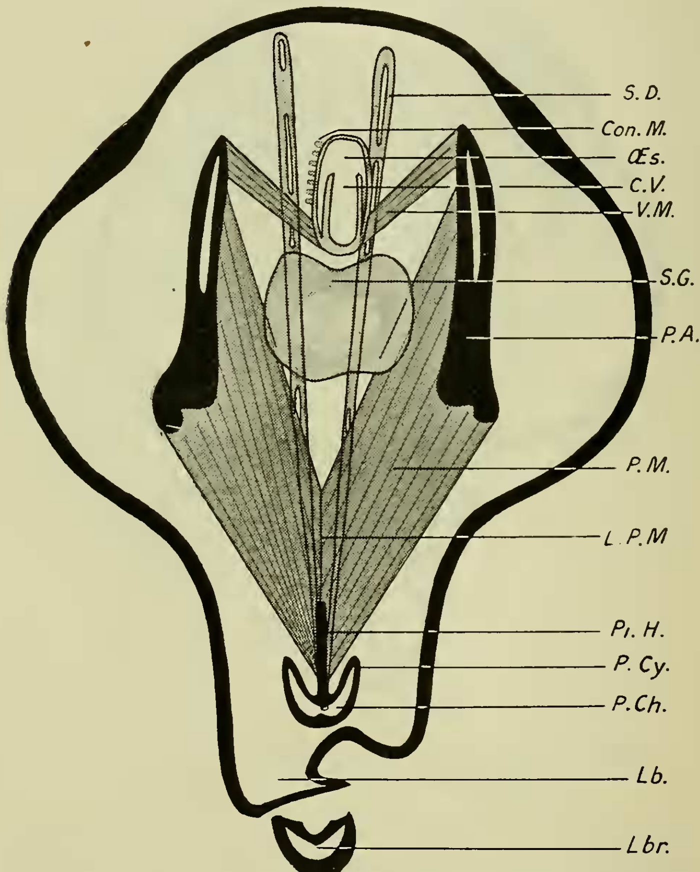
There is no trace of the maxillary groove upon the swollen bases, but it begins a little below. The structure of the groove is the same here as described in the external part, though on a minute scale. The stylets are, of course, separate in the head, as they pass one on either side of the pharynx (text-figs. 1, 5, 6, 11–19).

(*b*) The Mandibles. (Text-figs. 1, 5, 6, 23, Md.)

These are single structures from the beginning. The embryonic mandibles are the adult mandibles, there being no mandibular sclerite. The present view of their homologies has been given above.

Their external structure corresponds with that of the maxillæ. They lie just above them and do not go so deep into the head.

Text-figure 7.



Lygus pabulinus.

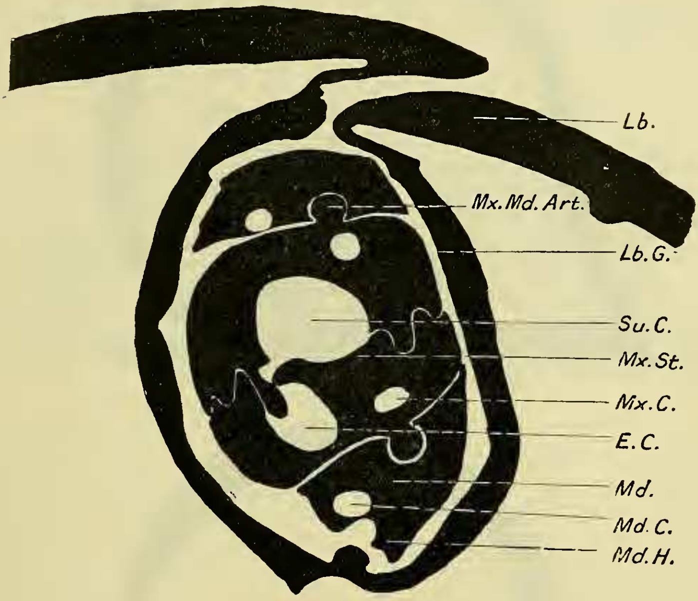
Reconstructed from numerous vertical sections, showing the relation of the muscles to the stylets, the pump, etc. Ob. 3 & Oc. 3.

For explanation of the lettering see p. 693.

They are flat and hollow and end in retort-shaped organs like the maxillary stylets; but unlike them :—

(i.) They never form tubes, as they do not unite and have no grooves on them. They are separate from end to end. Each of

Text-figure 8.

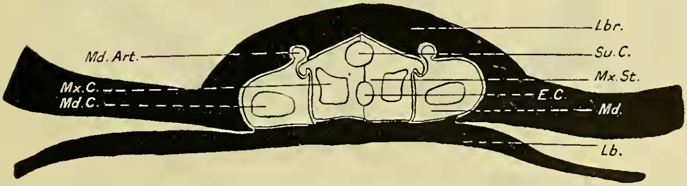


Lygus pabulinus.

Transverse section of the tip of the labium. Immersion-lens & Oc. 4.

For explanation of the lettering see p. 693.

Text-figure 9.

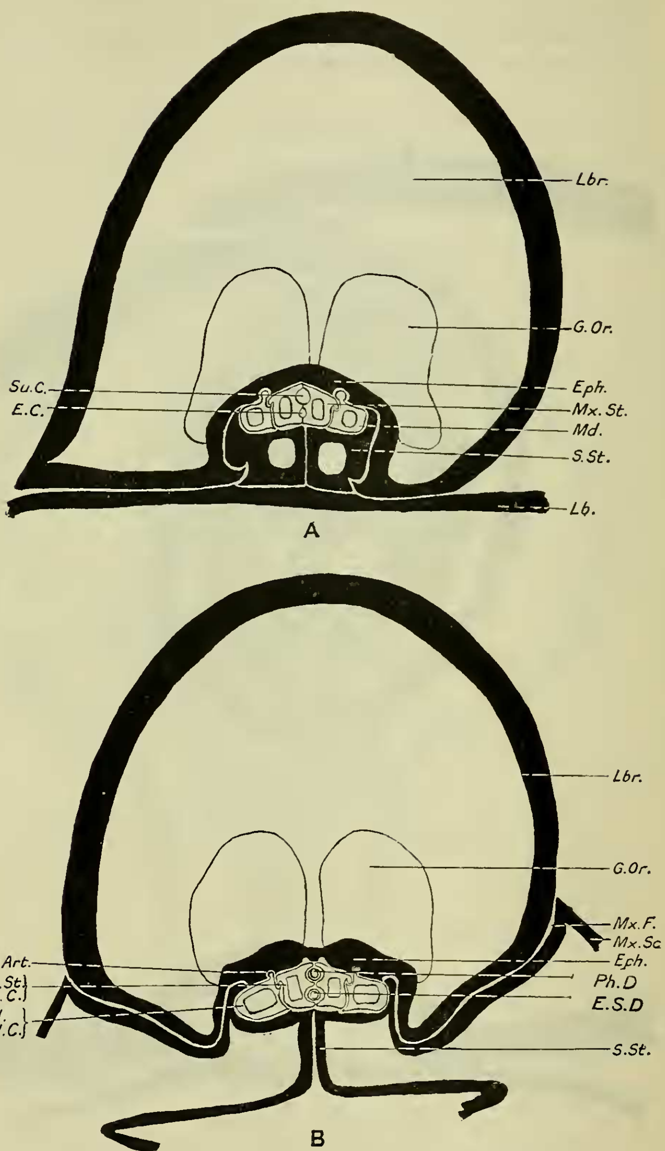


Lygus pabulinus.

Transverse section of the tip of the labium, showing the labrum and the labium enclosing the stylets. Immersion & Oc. 4.

For explanation of the lettering see p. 693.

Text-figure 10.



Lygus pabulinus.

A & B. Transverse sections, showing the epipharynx, gustatory organs, the pharyngeal duct, the efferent salivary duct, etc. Ob. 6 & Oc. 4.

For explanation of the lettering see p. 693.

them is connected with the maxilla of its side by an interlocking arrangement.

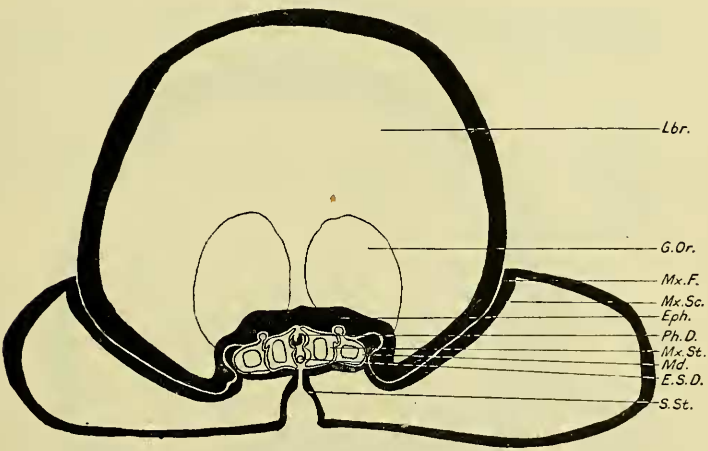
(ii.) The tips, which are pointed, are ornamented with recurved hooks, the number and size of which seem to vary in different species. The number varies from 7 to 9 in *L. pabulinus.* They are bigger towards the tips of the mandibles but get reduced posteriorly. The hooks will tear the tissues when withdrawn from them with the maxillary stylets, though this arrangement will not prevent their entrance into tissues. Their function will be clear later on (text-fig. 23, T.Md.).

(II.) Anatomy.

The stylets are chitinous, the chitin being lined by the chitinogenous epithelium which forms a continuous layer under it. Each of the stylets is enclosed in a sheath which is continuous with the integument of the head. This shows that both stylets have been invaginated in the course of their development, as is demonstrated by Heymons (text-figs. 4–7, Mx.Sh., Md.).

The retort-shaped organs. (Text-figs. 5, 6, 20, 21, Poc.Or.).—These are characteristic of the Rhynchota (Heteroptera and Homoptera). Mecznikow (**49**) has described them as the structures

Text-figure 11.



Lygus pabulinus.
Transverse section, showing thickening of the floor of the pharyngeal duct (*cf.* figs. 10 A and 12).
For explanation of the lettering see p. 693.

from which the new maxillæ and the mandibles are formed, but, as is shown above, they are not new structures at all. They are nothing, in fact, but the swollen bases of the stylets, the swelling being formed during development. They are the same as the Taschen-formigen structures of Heymons.

They are oval and curved laterally outward. They are found in the middle part of the head and show a curious structure in cross-sections, appearing as areas of glandular tissue surrounded by a chitinous ring which disappears in more distal sections.

The Interlocking Arrangement of the Stylets (*external and internal*). (Text-figs. 8–16, Mx.Md.Art., Md.Art.).—As shown by Davidson (9), the maxillæ and the mandibles of *Schizoneura lanigera* are round and lie loose from each other. In *Lygus pabulinus*, however, they are never separate outside the head, but are interlocked. Within the head the members of both pairs lie loose; the maxillæ and the mandibles being smooth and oblong without any processes (text-figs. 18–20, Md., Mx.St.). Anteriorly in the labral region, they have a different structure. The mandibles give rise dorsally to longitudinal ridges (which in section appear as knobbed processes), which attach them to the labrum or epipharynx. These disappear, however, beyond the labrum. This arrangement demonstrates the importance of the labrum in keeping the stylets in place and preventing their lateral sliding.

The maxillæ also have small processes, of a similar nature and function, which attach them firmly to the mandibles. These structures are clearly visible in cross-sections. In the fourth segment of the labium they are more pronounced.

It is obvious, therefore, that the mandibles and maxillæ are inseparably attached to one another, and, the space between them being exceedingly small, friction will ensure their simultaneously working up and down; the mandibles accompanying the maxillæ all the time and all the way in and out of the plant-tissues, unless a differential force be applied *. Inside the head they are always prevented from lateral movement by structures which are invaginations or infoldings of the outer walls of the head, and which enclose them successively at different levels.

These folds are formed by:—

(i.) The hypopharynx. (Text-figs. 13–15, Hyp.)
(ii.) The buccal fold. (Text-figs. 16–19, Bu.F.)
(iii.) The labial fold or the maxillary fold, formed by the infolding of the maxillary sclerite. (Text-figs. 16–19, Mx.F.)

These are very prominent structures in cross-sections of the head. They are not, however, found in the heads of those forms which require lateral movements of their mouth-parts, *i. e.*, in the biting insects.

The Tentorium or Endoskeleton.

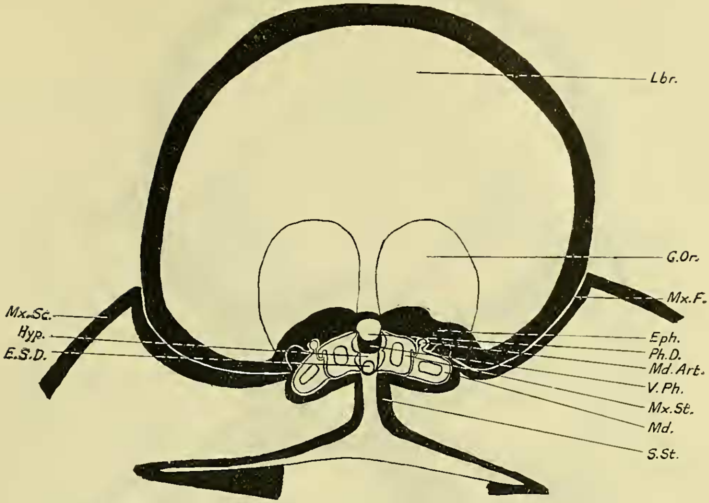
(Text-figs. 1, 4, 6, 7, 17, 19–22.)

This has already been described by various writers: Burmeister, Wedde, Léon, Bugnion, etc. Its description by Comstock and

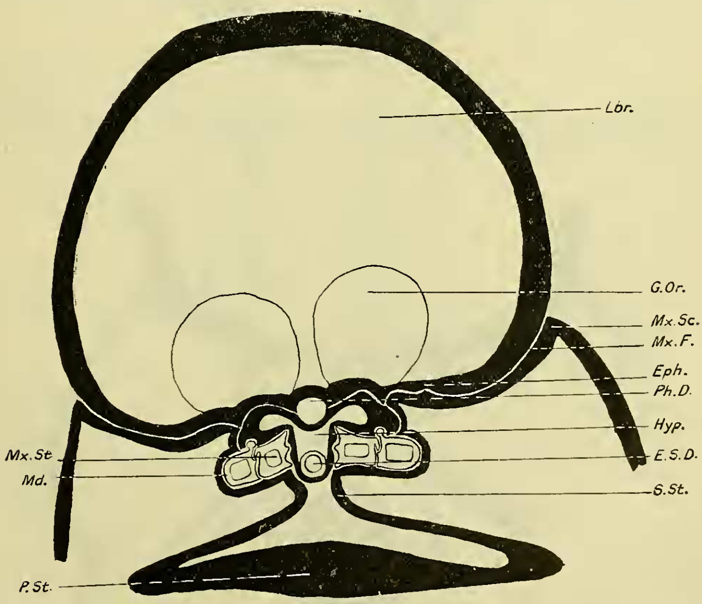
* The existence of such a force will be demonstrated later on.

Text-figures 12 and 13.

Lygus pabulinus.



Text-fig. 12.—Transverse section, showing the maxillo-mandibular articulation, the mandibular articulation, the pump-chamber, the pump-stem, etc. Ob. 6 & Oc. 4.

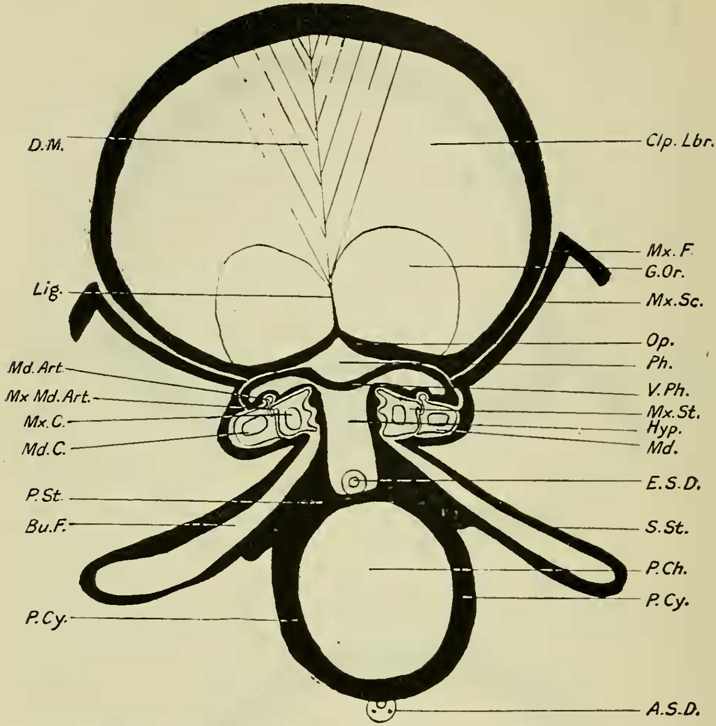


Text-fig. 13.—Transverse section, showing the maxillo-mandibular articulation, the mandibular articulation, the pump-chamber, the pump-stem, etc. Ob. 6 & Oc. 4.

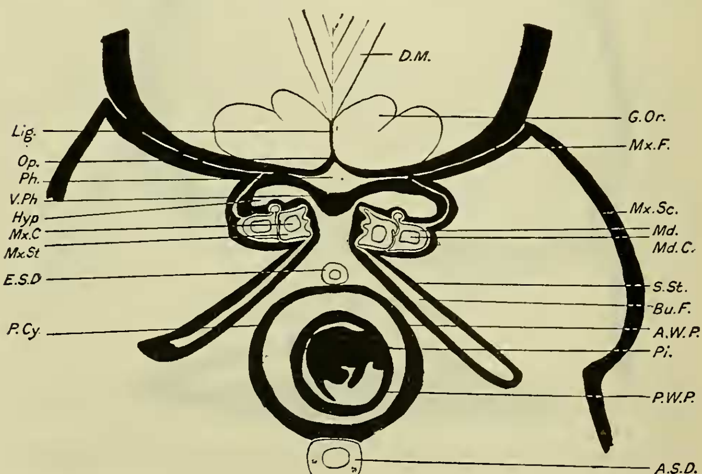
For explanation of the lettering see p. 693.

Text-figures 14 and 15.

Lygus pabulinus.



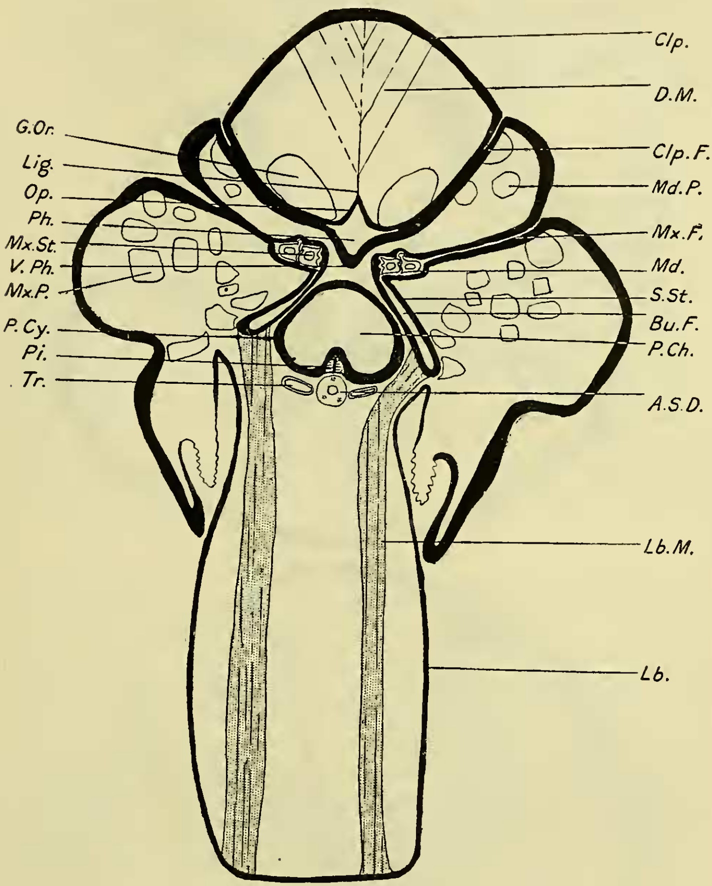
Text-fig. 14.—Transverse section, showing the maxillo-mandibular articulation, the mandibular articulation, the pump-chamber, the pump-stem, etc. Ob. 6 & Oc. 4.



Text-fig. 15.—Transverse section, showing the piston, the afferent salivary duct, the divaricators, the protractors of the stylets, the labial muscle, etc. Ob. 6 & Oc. 4.
For explanation of the lettering see p. 693.

Kocchi (6) has the special advantage of a simple terminology, which I have accordingly adopted here.

Text-figure 16.



Lygus pabulinus.

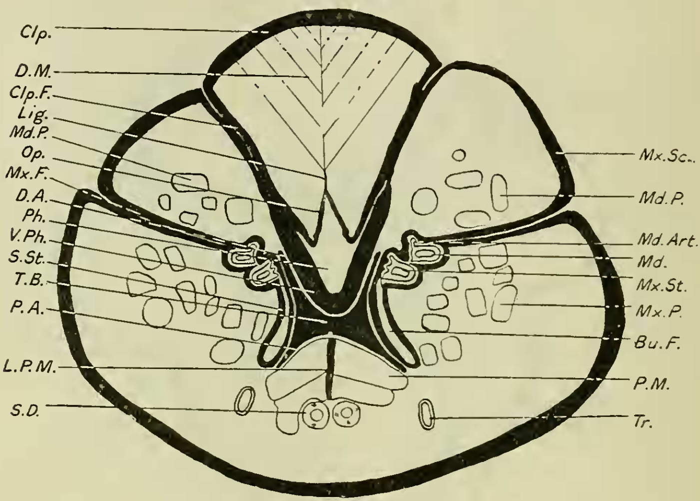
Transverse section, showing the piston, the afferent salivary duct, the divaricators, the protractors of the stylets, the labial muscle, etc. Ob. 3 & Oc. 4.

For explanation of the lettering see p. 693.

The endoskeleton of *Lygus pabulinus* consists of hollow chitinous rods which are covered by a thin hypodermal (chitinogenous) layer. They are nothing but involutions of the chitin of the head, and therefore are called "Apodemes." The fact that the tentorium consists of these hollow structures is very significant.

Great stresses have to be borne, and economy of skeletal material has been effected and a maximum of rigidity attained, by forming this material into hollow tubes instead of into solid rods. Many parallel cases may be instanced from the plant kingdom—of hollow stems which resist great stress.

Text-figure 17.



Lygus pabulinus.

Transverse section, showing the clypeal folds, salivary ducts. Ob. 2 & Oc. 12.
For explanation of the lettering see p. 693.

The tentorium consists of the following parts :—

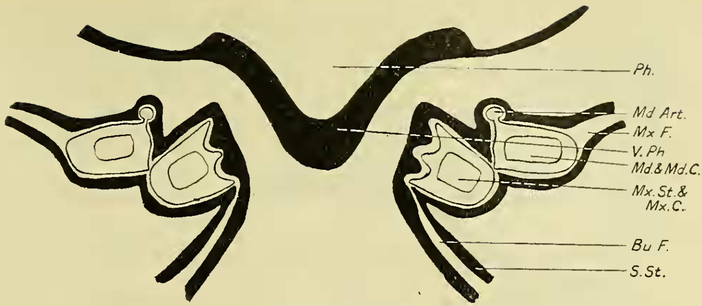
(I.) The Body of the Tentorium, or Tentorium proper. (Text-figs. 1, 4, 17, 19, T.B.)

This is formed by the fusion of the different arms of the endoskeleton. It lies between the pump below and the pharynx above. It is found at the place where, if it were absent, there would be great probability of the pharynx on the one hand and the pump on the other, being dragged out of their positions by contractions of their powerful muscles. It furnishes a firm support for both these organs.

Its structure is interesting; both its surfaces (dorsal toward the pharynx, and ventral facing the pump) are curved and form two grooves. The groove facing the pharynx is V-shaped and corresponds exactly to the shape of the ventral wall of the pharynx, which fits closely into it. They are joined together by connective tissue.

The shape of the other groove, *i.e.* the ventral one, is roughly semicircular, and into it the pump is wedged, and kept there by connective tissue.

Text-figure 18.



Lygus pabulinus.

Part of a transverse section, showing the stylets magnified, and their arrangement. Ob. 3 & Oc. 12.

For explanation of the lettering see p. 693.

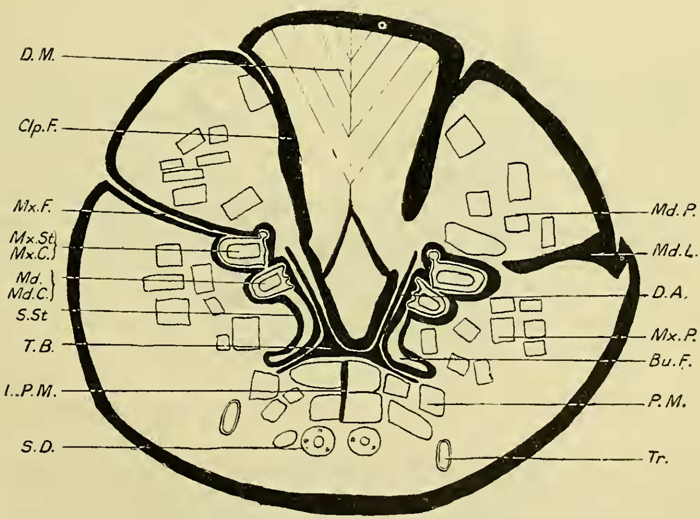
(II.) The Dorsal Arms. (Text-figs. 4, 17, 18, D.A.)

These are short and do not reach the walls of the head but lie free within it. The sides of the V (*i. e.*, the ventral wall of the pharynx) are firmly attached to these arms by connective tissue.

(III.) The Posterior Arms. (Text-figs. 1, 4, 5, 7, 20–22, P.A.)

These are more important than the dorsal arms. They run

Text-figure 19.



Lygus pabulinus.

Transverse section, showing the mandibular levers, stylets magnified, and their arrangement. Ob. 3 & Oc. 12.

For explanation of the lettering see p. 693.

posteriorly from the tentorial body to the posterior wall of the head. They are broad, elongate, and flattened dorso-ventrally. The pharynx is supported by them (text-fig. 20) just behind the tentorial body, their connection with the pharynx being through connective tissue.

At the far end, towards the wall of the head, the arms begin to bifurcate, one armlet going straight to the posterior wall and the other to the side of the head (text-fig. 5).

Their functions are very important in the mechanism of suction :—

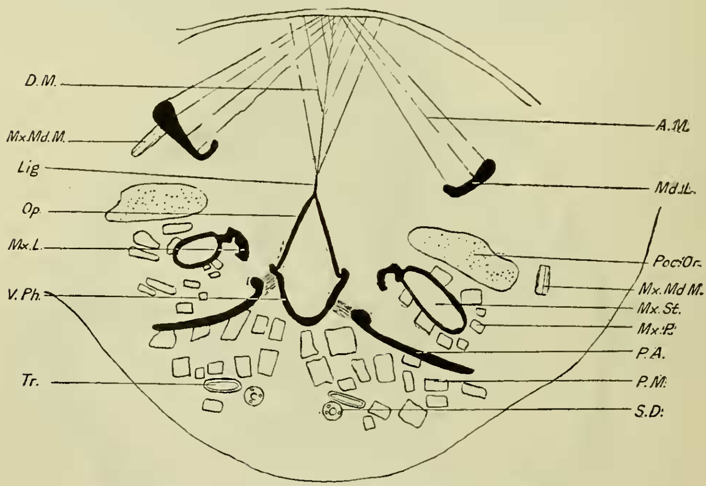
(i.) They support the pharynx at the place where there is great tension.
(ii.) The pump muscles are attached to them ventrally.
(iii.) The valvular muscles find support in them.
(iv.) The maxillary levers are supported by them.

It will be seen that the pharynx has support on all sides, *i. e.* ventrally, laterally, and dorsally (see below).

(IV.) The Levers. (Text-figs. 1, 5, 6, 19, 20, Mx.L., Md.L.)

Besides the tentorium proper, there are other chitinous structures which are connected to the outer and inner stylets. They

Text-figure 20.



Lygus pabulinus.

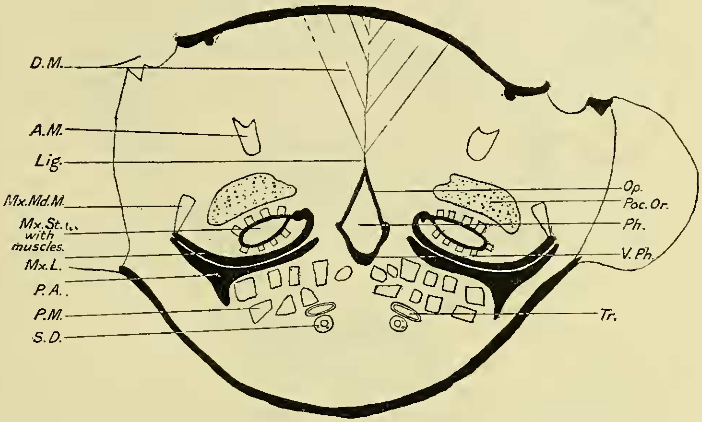
Transverse section, showing the antagonistic muscles, the retort-shaped organs, the posterior arms of the tentorium, etc. Ob. 3 & Oc. 12.
For explanation of the lettering see p. 693.

are known as the mandibular and the maxillary levers, and are placed at right angles to the direction of the stylets.

(A) The Mandibular Levers. (Text-fig. 19, Md.L.)

These are attached proximally to the lateral wall, or maxillary sclerite, just below the bases of the antennæ, and distally to the mandibles through a ligament. Their distal connection enables the levers to pull down the mandibles when the protractor muscles,

Text-figure 21.



Lygus pabulinus.

Transverse section, showing the maxillary levers, etc. Ob. 3 & Oc. 8.

For explanation of the lettering see p. 693.

which are attached to the former, contract. Proximally, at the bases of the levers, there is no hinge-like device but, on the contrary, they are fused with the sclerite. They are bifurcated distally, the mandibles passing through the fork.

Their functions are:—

(i.) They give attachment to the protractor muscles of the mandibles, which muscles are attached to the distal ends only.

(ii.) The maxillo-mandibular muscles are attached to them. (Text-figs. 20, 21, Mx.Md.M.)

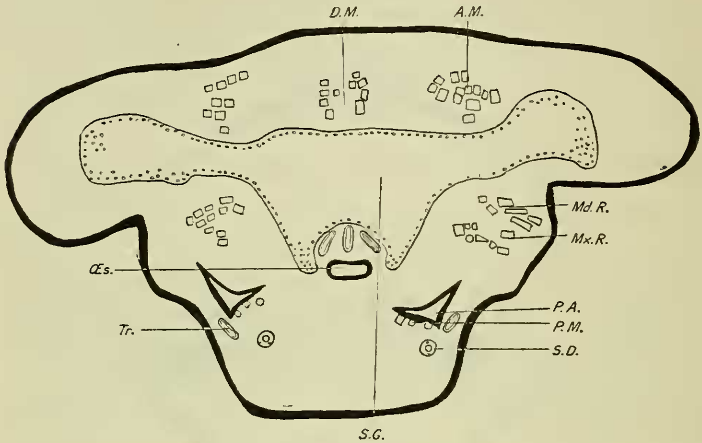
(iii.) The antagonistic muscles, which serve to bring back the levers to their normal positions, are also attached to them. (Text-figs. 5, 20, A.M.)

(iv.) The mandibles are supported by them.

(B) The Maxillary Levers. (Text-figs. 1, 5, 21, Mx.L.)

These are narrow and elongate, and have no connection with the lateral walls of the head. Their proximal attachment is to the posterior arms of the tentorium, and distally they are connected with the maxillæ. They taper gradually towards their bases, and are curved as they pass below the maxillary stylets, to which they are closely applied.

Text-figure 22.



Lygus pabulinus.

Transverse section, showing the supra-œsophageal ganglion, the retractor muscles, etc. Ob. 3 & Oc. 8.

For explanation of the lettering see p. 693.

Their relations are:—

(i.) They support the maxillary stylets.
(ii.) The maxillo-mandibular muscles are attached to them.
(iii.) They never give attachment to any of the maxillary muscles, which are attached to the maxillary stylets themselves.

The Muscles of the Head.

The musculature of the head is very complicated. The diversity of the muscles is correlated with the diversity of function of the structures which are required for effecting suction.

The groups of muscles are as follows:—

(1) *The Divaricators.* (Text-fig. 2, D.M.)

These muscles are attached to the upper wall of the pharynx; the mode of their attachment varying in different parts of the head. In the clypeal region they are attached to the ligament of the operculum (the upper wall of the pharynx); while in the epicranium they are attached to the pharynx directly.

I find that these muscles are strengthened by chitinous rods comparable perhaps to the tendons in the muscles of the vertebrates (text-fig. 2).

These muscles fall into two groups, according to the mode of their attachment and arrangement:—

(*a*) The fan- or feather-shaped muscles. (Text-figs. 14–21).—These are arranged like barbs on a feather vein or rachis, alternating with one another on either side. This arrangement begins in the clypeal region and gradually disappears posteriorly. They are attached to the opercular ligament, which is the continuation of the soft chitin lining the operculum. In the clypeo-labral region, *i. e.*, in the region where the gustatory organs are situated, the ligament passes between those organs to give attachment to these muscles. The gustatory organs consist of four lobes arranged in pairs on either side of the dorsal wall of the pharynx. (Text-figs. 27, 28.)

The fan-shaped arrangement is found in the region where there is a great amount of work done; the work being to produce a vacuum sufficiently powerful to suck in the sap which is being accumulated in the pharyngeal duct. This vacuum is produced by contractions of these muscles, the operculum being pulled out of the ventral wall of the pharynx. The arrangement described gives a large surface for the attachment of the muscles.

(*b*) The strap-shaped muscles.—These are found in the epicranial region, where they are directly attached to the upper wall of the pharynx, which has here lost its character of operculum. Here its ventral wall also loses its chitin, and the whole structure is gradually transformed into the soft and thin œsophagus which is no longer concerned with suction. These muscles are attached to the dorsal wall of the head in the median line.

The divaricators occupy a large area in the head, beginning in the clypeo-labral region and ending in the anterior part of the epicranium.

(2) *The Pump muscles, or Aspirators.* (Text-figs. 2, 4, 5, 7, 17, etc. P.M.)

These are next to the divaricators in order of importance, though they do not occupy such a large space. They are very compact and powerful, as may be seen from the mode of their arrangement and attachment. They lie below the pharynx in the median line, but they diverge on either side towards the posterior arms of the tentorium, to the ventral surface of which they are fused. At the other end they are attached to the handle of the piston of the pump.

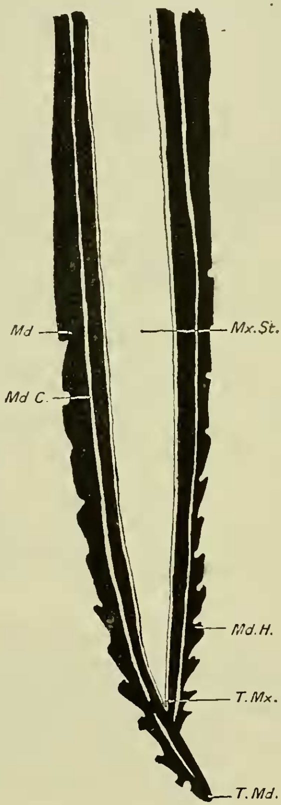
When they contract they pull out the piston of the pump, the posterior arms of the tentorium being very strong and rigid at the sides. This pulling out cannot be an easy thing, small as the pump is, because the posterior wall, of which the piston forms a part, is made of thick, unyielding, though elastic, chitin, the resistance of which must be enormous. Hence their disproportionate size and the mode of their attachment can easily be understood.

(3) *The Protractors of the Stylets.* (Text-fig. 6, Mx.P., Md.P.)

(*a*) The Protractors of the Mandibles. (Text-figs. 16, 17, 19, etc., Md.P.)

These muscles are attached at one end to the distal ends of the levers of the mandibles (and not to the mandibles themselves), and at the other to the clypeal folds, which run into the head to a considerable distance. They are short and thick, and run obliquely

Text-figure 23.



Lygus pabulinus.

Tips of the stylets, showing the recurved hooks of the mandibles and smoothness of the maxillary stylets. Immersion-lens & Oc. 4.

For explanation of the lettering see p. 693.

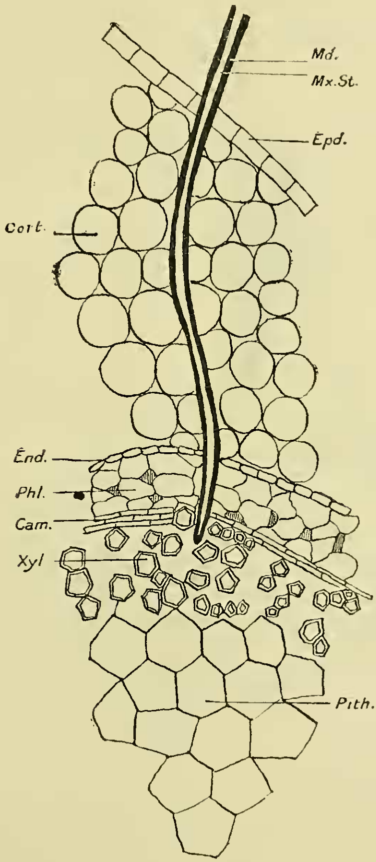
from one to the other. Their attachment at the distal ends of the levers makes it easy to pull the latter down with the mandibles. There is no hinge-like device at the bases of the levers, but when they are pulled down they do not, I think, regain their normal positions by their own elasticity alone or that of the side-walls of the head. They are brought to their original positions by the antagonistic muscles.

The protractors are the chief agents in bringing about protrusion of the mandibles.

(*b*) The Protractors of the Maxillæ. (Text-figs. 16, 19, 21, etc., Mx.P.)

They are attached at one end to the sides of the maxillary

Text-figure 24.



Lygus pabulinus.

Hand section, showing the stylets in the plant-tissue. Stained with saturated picric in 90 per cent. alcohol. Ob. 3 & Oc. 4.

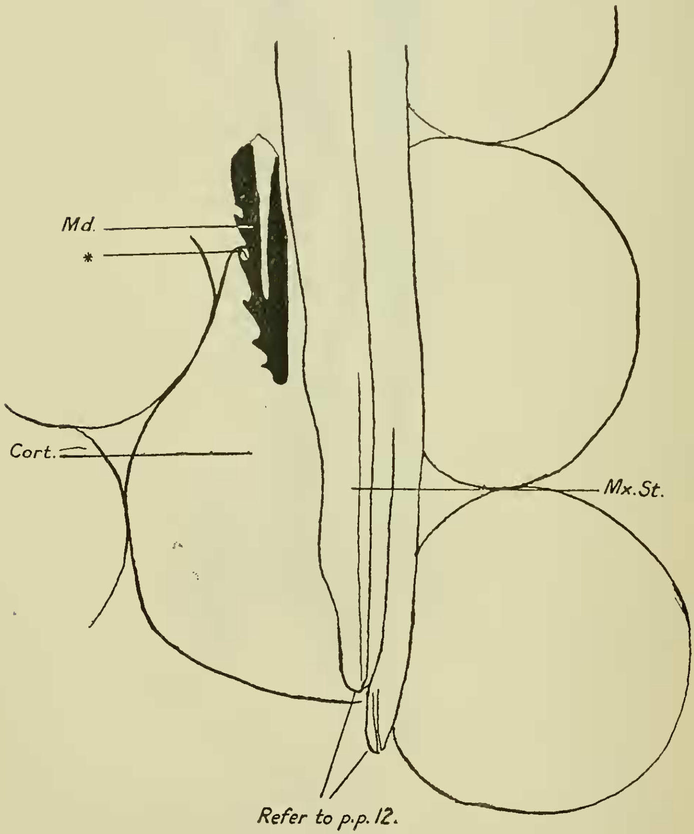
For explanation of the lettering see p. 693.

stylets (and not to the levers), and at the other to the maxillary sclerite. It has been shown above that the latter is nothing but the maxillary plate, the second half of the embryonic maxilla.

(4) *The Retractors of the Stylets.* (Text-figs. 16, 19, 21.)

These are attached to the sides of the mandibles and the maxillary stylets just below the retort-shaped organs at one end, and to the posterior walls of the head at the other. The stylets show peg-shaped structures for the attachment of the muscles

Text-figure 25.



Lygus pabulinus.

Transverse section of a petiole, showing the maxillary stylets forward and the mandibles behind, one of the hooks (*) of the latter being attached to the cellular wall. Immersion lens & Oc. 4.

For explanation of the lettering see p. 693.

(text-fig. 6), which are spread at their other ends over a large part of the posterior wall of the head.

The retractors of the mandibles consist of two groups which pass above and below the optic nerve (text-fig. 5).

(5) *The Maxillo-mandibular Muscles.* (Text-figs. 20, 21, Mx. Md.M.)

These run from the mandibular levers to the levers of the maxillary stylets on either side. It will be remembered that the mandibles and the maxillary stylets do not lie at the same level, one being above the other, and at the same time the maxillary stylets project further back into the head than the mandibles. In the normal position the tips of the mandibles and the maxillary stylets are level, and in this position they are thrust into the plant-tissue.

When these muscles contract, they pull in the mandibles and push forward the maxillary stylets a little. Thus there is no hindrance to suction by the maxillæ, as they are free from the mandibles. At the same time the mandibles get themselves fixed into the cellular walls by means of their recurved hooks and thus steady the maxillæ for suction, as the latter are firmly attached to the former by the interlocking device. Thus these muscles play a useful part in the mechanism of suction.

(6) *The Antagonistic Muscles.* (Text-figs. 5, 6, 20, A.M.)

These muscles are attached to the mandibular levers at one end and to the postero-dorsal wall of the head at the other. They are called antagonistic because they oppose the protractors of the mandibles in their action, inasmuch as they bring the levers back to their normal positions. They are very important, as there is no other device to effect this readjustment.

They have nothing to do with the pharynx, as Bugnion and Popoff (**4**) seem to think, who describe these muscles as "Antagonistique ou Abaisseur du Pharynx." The description that they are attached to "une lame horizontale rattachée au Pharynx par une expansion," is absolutely inaccurate. This horizontal blade (lame) is nothing but the mandibular lever, which has nothing to do with the pharynx, but which is attached to the mandible. "La lame horizontale tendant à effectuer un mouvement de bascule, l'effet de l'antagoniste doit être d'abaisser le pharynx ou tout au moins de le maintenir en place au moment où le dilatateur entre en action." "La fonction du muscle antagoniste est de maintenir l'appareil en place." With due respect to these authors, I think that their description is absolutely beside the mark. These muscles have nothing to do with the pharynx. Wedde, however, holds that there is no need for such antagonistic muscles of Bugnion. He says, "Antagoniste für die Schlundmuskulature sind nicht vorhanden, es wirken als solche die höchst elastichen chitinteile des Pharynx selbst."

Wedde, however, thinks that they are the clypeal muscles, which have nothing to do with the mandibular levers, but which are attached to them. He does not seem to have understood the nature of the "horizontal bar," which is nothing less than the mandibular lever.

(7) *The Constrictors or Circular Muscles.* (Text-figs. 2, 7, Con.M.)

These muscles are found in the œsophageal region. They lie outside the external epithelium of the œsophagus. Their contraction and relaxation produce a kind of peristalsis which forces the sap onward into the stomach. Bugnion (**4**) says, "quant au constricteur, son role doit être de pousser dans l'œsophage le liquide absorbé."

(8) *The Valvular Muscles.* (Text-fig. 7, V.M.)

They are short and thin and extend from the base of the cardiac valve in the œsophagus to the posterior arms of the tentorium, to both of which they are attached. When they contract, the sides of the valve are pulled apart, the valve thus opens, the lumen of the œsophagus widens, and the sap, which is under a great pressure behind, is forced onward into the stomach. I cannot find them described by any previous writer.

(9) *The Labial Muscles.* (Text-figs. 2, 16, Lb.M.)

These are found in the first segment of the labium, and seem to be important in increasing the amount of protrusion of the stylets by bending the labium. They are attached at one end to the supporting struts (buccal folds) on either side of the pump-cylinder, and at the other to the first joint of the labium, which is swollen, and thus offers a large area for the attachment of these muscles.

It will be remembered that the proboscis bends upon itself, the bending occurring at the first joint. The deeper the required plant-tissue lies, the greater is the bending of the proboscis. There must be some device to effect this bending, and such a device is supplied by these labial muscles. When the muscles contract, the first joint is pulled up and acts as a hinge—the proboscis bending on it.

According to Geise, Wedde, and Nietsche they are elevators and depressors of the labium. In the insect under consideration no muscles are found that could possibly function in this way.

(10) *The Muscles of the Antennæ.*

As these have nothing to do with suction, they will not be described.

N.B.—Wedde has described two pairs of protractor muscles of the maxillary stylets, one of which is attached to the maxillary sclerite, the other passing below the pharynx. It seems that the latter pair does not represent the protractors but the pump muscles.

The Pharynx, or Schlundkopf. (Text-fig. 2.)

This is one of the interesting and characteristic organs of the Rhynchota. In transverse sections it resembles roughly the pharynx of a sucking Dipterous insect (Nuttall and Shipley (**40**)). There are, no doubt, some differences in each case, but the general plan is the same throughout. In all these cases suction is effected by the production of a partial vacuum inside the pharynx, in order to fill which the sap or blood flows up the proboscis.

The pharynx is a long, chitinous organ with a narrow lumen. Its structure varies in different regions of the head, and therefore it is proper to treat its several parts under different names.

There are three distinct modifications in different regions:—

(i.) The Pharyngeal duct, in the clypeal region, where the operculum as such does not exist, and the whole structure—here formed from the lower wall of the pharynx alone—forms one round duct which opens into the suction-canal. (Text-figs. 11–13, Ph.D.)

(ii.) The Pharynx proper, in the clypeal region and the anterior part of the epicranium, where its upper wall, as the operculum, is clearly distinguishable. (Text-figs. 14–21, Ph.)

(iii.) The Œsophagus, in the epicranial region, where the walls of the pharynx are soft, and the operculum as such disappears. (Text-figs. 2, 22, Œs.)

(i.) *The Pharyngeal duct.*

This is the continuation of the pharynx proper into the labral region where it opens into the suction-canal. It is the modified pharynx, the modification consisting in a gradual elimination of the epipharynx from the upper wall of the pharyngeal duct, from behind forward. The lower wall at the same time gradually gets thinner and more rounded and ultimately forms a duct by itself. The divaricator muscles of the pharynx have disappeared with the operculum. At the place where the pharynx ends and the duct begins there are found the gustatory organs communicating with the lumen of the duct through the cribriform plate (text fig. 26, G.Or., Cri.Pl.) In this region the hypopharynx (text-figs. 13, 14, Hyp.) is well developed, forming a folded structure supporting the maxillary stylets and the mandibles laterally, and enclosing the efferent salivary duct underneath. It supports the pharyngeal duct in the region where it has no other support, neither that of the body of the tentorium nor that of the tentorial arms. Anteriorly the hypopharynx becomes smaller and smaller and less folded. It brings the efferent salivary and the pharyngeal ducts nearer to each other (text-figs. 11-13, Ph.D., E.S.D.), and finally disappears, leaving free these ducts, which open ultimately into the suction- and the ejection-canals respectively (text-figs. 10 A and 10 B).

The pharyngeal duct runs to a considerable distance into the suction-canal before it ends. The importance of this arrangement lies in the fact that it makes allowance for the movements—up and down—of the maxillary stylets. Had this duct run to a shorter distance into the suction-canal, there would have been some danger of its slipping out when the stylets were pushed down to their natural limit of extension.

(ii.) *The Pharynx proper.*

This is found to begin in the clypeal region behind the clypeal folds and to end in the anterior part of the epicranium. It is bent anteriorly, and its bend corresponds to that of the head. Posteriorly it is straight and runs directly into the œsophagus. It is different in structure from the pharyngeal duct and from the œsophagus. It is the chief organ of suction in the insect.

When seen in transverse section it consists of two distinct parts: the ventral part and the dorsal. The first may be called the "V" and the second the operculum. They are different in shape and structure. (Text-figs. 14-21.)

(a) *The "V" or ventral wall of the pharynx* (V.Ph.).—This is more or less V-shaped in section, its angle being considerably drawn out in some places. In the anterior and the posterior regions this angle gets rounder, and the characteristic form of the "V" is lost, as in the pharyngeal duct and the œsophagus. In the clypeal region, where the pharynx proper begins, the arms of the "V" are elongated and fused with the clypeal folds running into the head (text-figs. 16, 17, 19, Clp.F.). Thus it is dorsally supported by these folds.

In the same region, moreover, the "V" is wedged ventrally into the body of the tentorium and retained there by the connective tissue, its ventral shape corresponding exactly to the dorsal groove in the latter (text-figs. 17, 19, T.B., V.Ph.). The dorsal arms of the tentorium run parallel with those of the "V" and support it laterally. It is this part of the pharynx which needs support because it is here that the sucking force is applied.

The posterior arms of the tentorium as they run backward also support the pharynx to some extent, but they soon diverge laterally and leave it (text-fig. 20, P.A.).

The "V" is of thick chitin which, however, becomes thin and soft anteriorly and posteriorly in the pharyngeal duct and the œsophagus.

(b) *The Operculum or dorsal wall of the pharynx* (Op.).—Its structure is entirely different from that of the "V". It is closely apposed to the "V" in its normal position, which is regained by its own elasticity, and from which it is pulled by contraction of the divaricator (pharyngeal) muscles. It is obvious that there is no space left in the lumen of the pharynx when the operculum is in the normal position, but a strong vacuum is produced in it when it is pulled out.

It is lined with a thin and soft chitin which is continued dorsally into a ligament to which the divaricators are attached.

Posteriorly it loses its character as an operculum (text-fig. 22); it is no longer introversible though it remains flexible. The "V" and the operculum form together, in this posterior part, one structure, which is more or less circular and is continued in the œsophagus. In this region the muscles are directly attached to it instead of to the ligament. As it passes anteriorly into the pharyngeal duct it also loses its flexibility and introversibility. It fuses with the epipharynx (labrum) which now covers the ventral wall, and the muscles are again no longer attached to it. Thus in both directions (anteriorly and posteriorly) the pharynx proper loses its character as such, both in respect of the "V" and the operculum.

There is a hinge-like fold of chitin upon which the operculum turns inside out. It will be understood from the figure (text-fig. 20).

The supports of the pharnyx proper are:—

(i.) The hypopharynx.
(ii.) The clypeal folds.
(iii.) The body of the tentorium with its dorsal arms.
(iv.) The posterior arms of the tentorium.

All these supports make the "V" immovably and firmly fixed in its proper place, while the operculum remains all the time flexible and introversible.

The function of the pharynx proper is very important since it is the chief organ of suction. The pharyngeal duct cannot start suction as there are no muscles attached to its dorsal wall, which is no longer introversible; as explained above the operculum in its normal position is closely apposed to the "V," and thus there is no empty space between them. The muscles contract, the operculum is pulled out, and a strong vacuum is produced. To fill it up, the sap, which is now present in the pharyngeal duct, is sucked into it.

(iii.) *The Œsophagus.*

There is no sharp external demarcation between the pharynx proper and the œsophagus, the transition is gradual, the "V" and the operculum losing their characteristic structures. In some other species there is, at the entrance to the œsophagus, a constriction, which is due to the fact that the thick chitin of the pharynx proper ends suddenly where the œsophagus begins. The nerve-mass, consisting of the supra-œsophageal ganglia, the lateral commissures, and the sub-œsophageal ganglia, surrounds the œsophagus, which then opens straight into the stomach through the cardiac valve.

The œsophagus is lined with the layers of an epithelium, and, innermost of all, a soft chitin, which disappears posteriorly: from this point, the outer layer of the œsophagus is generally one cell thick, the cells being small. The inner layer consists of elongated cells which have vacuoles in them, and which are greatly developed in the stomach. Outside the outer epithelial layer are found the constrictor and the valvular muscles. (Text-fig. 2, Con.M., V.M.)

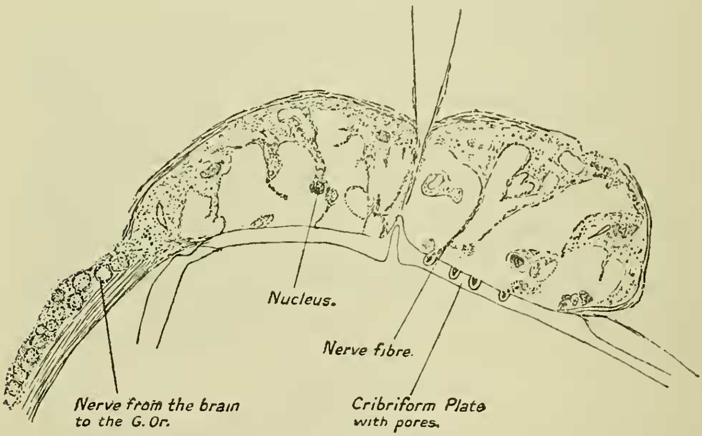
The Cardiac Valve (text-figs. 2, 7, C.V.)—This is very short, and it seems that its position in the œsophagus varies in different insects. In *Schizoneura lanigera* it is present at the end of the œsophagus (Davidson (**9**)), but in *Lygus* the valve is in its middle. It is formed by the doubling of a part of the œsophagus upon itself. The valvular muscles are attached to the base of the valve. It remains closed in the normal position until the muscles contract, when it is opened.

It prevents any return-flow of the sap from the stomach into the œsophagus.

THE GUSTATORY ORGANS. (Text-figs. 26–28.)

That these are a specialised part of the supraœsophageal ganglia is proved beyond doubt. They are situated upon the

Text-figure 26.



Lygus pabulinus.

Longitudinal section, showing the histological structures of the gustatory organs with the cribriform plate, etc. Ob. 6 & Oc. 4.

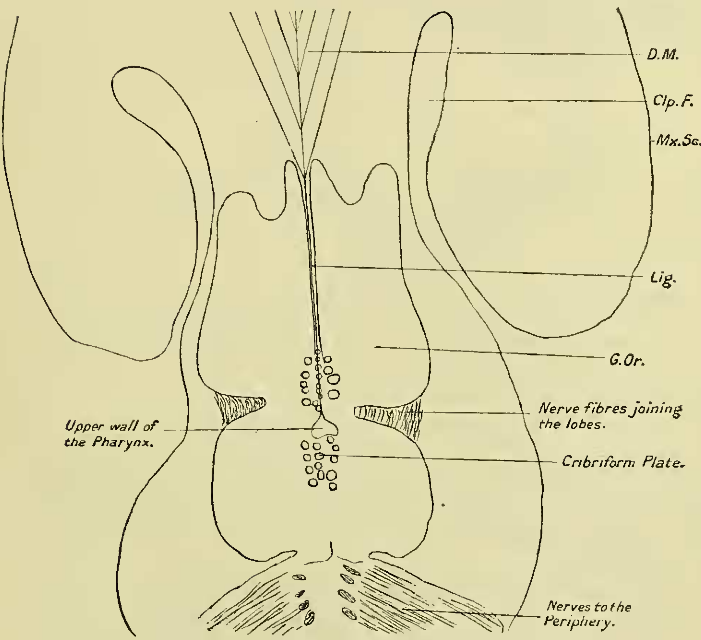
For explanation of the lettering see p. 693.

operculum in the clypeo-labral region. There is a nerve running from the brain to these organs on the upper wall of the pharynx. Their histological structures, though specialised, are similar to those of the brain.

In vertical sections, they show four lobes, arranged in pairs on either side of the operculum. The ligament passes through them to give attachment to the divaricators (text-figs. 27, 28, G.Or., Lig.). There are nerve-fibres running into the pharynx, and also from one lobe to the other. There are, moreover, small nerves issuing from them and distributing themselves over the epipharyngeal region.

The Cribriform Plate (text-figs. 27, 28, Cri.Pl.).—The chitinous plate upon which these organs are situated is perforated, and through it the nerve-fibres communicate outward

Text-figure 27.



Lygus pabulinus.

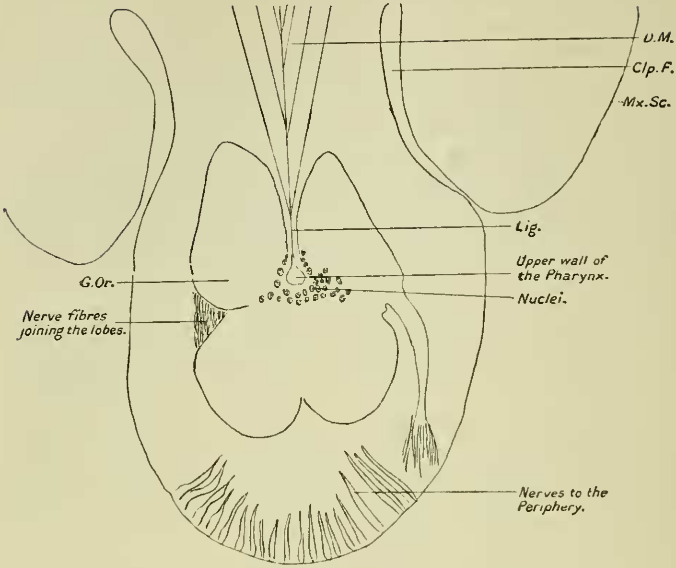
Vertical section of the gustatory organs with the cribriform plate, showing nerves passing to the periphery, etc. Ob. 6 & Oc. 4.

For explanation of the lettering see p. 693.

with the lumen of the pharynx. This cribriform plate seems to be analogous with that found in the mammals, in which the olfactory nerve-fibres pass through its pores to the olfactory sense-organ.

These organs seem to be gustatory. Their function seems to be to taste the sap as it comes into the pharyngeal duct.

Text-figure 28.



Lygus pabulinus.

Vertical section of the gustatory organs with the cribriform plate, showing nerves passing to the periphery, etc. Ob. 6 & Oc. 4.

For explanation of the lettering see p. 693.

The Pump-apparatus, or Wanzen-spritze.

This apparatus is one of the characteristic structures of the Rhynchota, and has been described, though not in detail, by many writers. It was first discovered by Landois (**28**) in *Cimex*, and described later on by Wedde (**46**), in some detail, in *Pyrrhocoris*.

It has been found in almost all rhynchotous forms except the Anoplura. Wedde has attached so much importance to it as to divide the Hemiptera into two groups: (i.) Rhynchota setifera—with the pump-apparatus, and (ii.) Pediculidæ—without it. It is possible that, in the Pediculidæ, it may have escaped the notice of investigators, since it must be very minute. I am the more encouraged in this belief because Grove (**16**) says that the pump-apparatus is not found in *Siphonophora rosarum* (a tolerably big form), though he has figured it in his drawings (fig. 7 *loc. cit.*). He further says, "In exactly the same position in the small pointed under-lip . . . . which closes the mouth on its posterior margin, where the above authors have described the salivary pump, is a small U-shaped rod of solid chitin." This small rod of solid chitin is nothing but the pump-cylinder.

The pump may conveniently be divided into four parts for description :—

(i.) The pump-cylinder with the pump-chamber and the pump-stem. (Text-figs. 2, 3, 7, 14, 15, 16, P.Cy., P.Ch., P.St.)

(ii.) The piston with the handle. (Text-figs. 15, 16; Pi., Pi.H.)

(iii.) The efferent salivary duct. (Text-figs. 3, 10–15, E.S.D.)

(iv.) The afferent salivary duct. (Text-figs. 2, 3, 16, etc. A.S.D.)

(i.) *The pump-cylinder with the pump-chamber and the pump-stem.*—The pump-chamber is more or less oval in section, and its thick and rigid chitinous lining (constituting the pump-cylinder) consists of two walls, an anterior and a posterior, which differ from one another in structure and shape, though there is no discontinuity of chitin between them.

(*a*) The anterior wall (A.W.P.). This is roughly semicircular in section. Its middle portion is drawn out anteriorly into a thickened solid process, which fuses with the hypopharynx, and this thick portion of the pump is known as the pump-stem (text-fig. 3, P.St.), which is perforated by the efferent salivary duct. The chitin of the anterior wall is thick, elastic, and incompressible. It gets, however, thinner laterally, and is continued into the posterior wall dorsally; but ventrally it lines the entrance of the afferent salivary duct.

(*b*) The posterior wall. This is apposed to the anterior wall in the normal position. Its middle portion is swollen and is called the piston. This is continued backward to form the handle. Its chitinous lining is elastic, introversible, and can be retracted from the anterior wall to a certain extent when the pump muscles act. These muscles have already been described above.

(*c*) The pump-chamber. The space between the walls, anterior and posterior, of the pump-cylinder constitutes the pump-chamber. In the normal position, when the posterior wall is apposed to the anterior, its capacity is reduced to a minimum. Introversion, of course, increases this capacity. Into the chamber opens antero-ventrally the afferent salivary duct, and from it issues antero-dorsally the efferent salivary duct, which latter finds its way out through the pump-stem to open into the ejection-canal of the maxillæ. (Text-figs. 3, 10 B., P.Ch.)

(*d*) Attachment. The pump-cylinder is attached by connective tissue to the body of the tentorium, which is situated just above it; the ventral groove of the tentorium corresponds exactly to the dorsal semicircular contour of the pump-cylinder. The attachment of the cylinder to the hypopharynx through the pump-stem has already been mentioned under (*a*).

(ii.) *The piston with the handle.*—The middle portion of the posterior wall is swollen and continued backward to a considerable distance as a solid rod of chitin. To this the pump muscles are attached. This structure constitutes the piston and the handle, the swollen portion being the piston and the backward continuation the handle. The latter is flattened dorso-ventrally.

(iii.) *The efferent salivary duct.*—This is a long and narrow duct, issuing antero-dorsally from the pump-chamber. It has a very narrow lumen and runs through the pump-stem and perforates the hypopharynx before it opens anteriorly into the ejection-canal. It has been shown above that the pharyngeal duct also runs through the same region of the hypopharynx on its way to the suction-canal. These ducts are thus brought together and connected with one another by the hypopharynx. It is the only connection between them; otherwise they are distinct from each other. They do not communicate with one another. And yet there are many misrepresentations about it. Many of the previous writers are very doubtful of the facts, and do not seem to know whether the efferent duct runs straight into the ejection-canal or the labial groove, or opens into the pharyngeal duct. Muir and Kershaw (**22**) write: "The syringe or salivary pump . . . opens on the basal part of the labium beneath the hypopharynx." This statement is too vague to be criticised. According to them, it seems that the efferent salivary duct opens into the labial groove. The same mistake has been made by Grove (**16**), and is also found in many text-books. The efferent salivary duct opens neither into the labial groove nor into the pharyngeal duct, but, on the contrary, runs straight into the ejection-canal and opens there. In short, the ducts, pharyngeal and efferent salivary, are separate from one another and open into the suction- and ejection-canals of the maxillary stylets respectively. (Text-fig. 10, Su.C., E.C.)

The efferent duct is supported by

(i.) The pump-stem, and
(ii.) The hypopharynx.

It runs a considerable distance into the ejection-canal before it ends. This prevents its slipping out of the canal when the maxillæ are pushed down by their protractors. (*Cf.* pharyngeal duct.)

(iv.) *The afferent salivary duct.*—The two salivary ducts issuing from the reservoirs on either side come together in the head and form the afferent or common salivary duct under the brain. This afferent duct is seen, in median longitudinal sections, running underneath the pump-cylinder and opening antero-ventrally into the pump-chamber. It has a lumen bigger than that of the efferent salivary duct, and its walls are flexible and elastic. There is not a trace of a valve at its entrance into the pump-chamber.

The salivary ducts (text-fig. 7, S.D.)—There are two salivary ducts, one on each side, issuing from the salivary reservoirs in the thoracic region. They are narrow and long, and run straight into the head, where they join together and form the common salivary duct. They are always full of secretion, and as they are thin and elastic, their walls are distended. The secretion is therefore under pressure.

The Function of the Pump.

The structures of the pump, described above, will show that it is used to force the salivary secretion forward into the efferent salivary duct and thence into the ejection-canal of the maxillary stylets. Hence it has been called a force-pump.

The ejection-canal pours the secretion straight into a wound in a leaf made by the stylets. The secretion does not leak out since the canal is air-tight, which will be seen from cross-sections. The shape of the cylinder in different species depends upon the degree of force required to drive the secretion through the efferent duct. The more minute this duct the more cylindrical is the pump: the return-stroke of the posterior wall is more powerful in proportion to the force required to pull out the piston. The posterior wall of the pump may be compared to a bow.

In the normal position the posterior wall is apposed to the anterior, and the capacity of the chamber is reduced to a minimum. When the pump muscles, which are attached to the handle, contract, the piston is pulled out and with it the posterior wall. The capacity of the chamber slowly increases and a partial vacuum is produced. Now, either the secretion from the efferent duct or that from the afferent duct must flow into the chamber to fill up this vacuum. The former case is impossible, as the efferent duct is very short and empties itself into the ejection-canal as soon as it is charged with the secretion, and when empty its lumen would tend to collapse owing to the thinness of its walls. On the other hand, the salivary ducts are always full of secretion under pressure, and their walls are always distended by their contents. As soon, then, as a vacuum is produced in the chamber, the secretion in the afferent duct flows forward into it. Thus, every time the muscles contract and the vacuum is produced, fresh secretion from the reservoirs flows into the pump-chamber.

When the muscles relax, the posterior wall of the cylinder begins to return to its former position, the return-stroke being effected by its own elasticity. The fluid in the chamber is gradually being compressed, and is forced along the line of least resistance, which lies through the efferent salivary duct. This duct is empty now, while the afferent duct is full of secretion under pressure. The secretion therefore must flow into the efferent duct. The space of the chamber is gradually being reduced, and the entrance of the afferent duct into the chamber is closed when that critical point is reached at which the pressure inside the chamber becomes higher than that in the afferent duct. This closure is effected by the posterior wall itself, which slides over and closes the entrance to the duct. Thus there is no necessity for a valve, and the saliva, once in the chamber, never flows back into the afferent duct.

To sum up:—

(i.) The pump is a force-pump.

(ii.) The return-stroke of the posterior wall is effected by its own elasticity, when it has been pulled from the anterior wall by the pump muscles.

(iii.) The efferent salivary duct is short and empties itself into the ejection-canal as soon as it is charged with secretion. It is therefore empty when the return-stroke begins.

(iv.) The afferent salivary duct is always full of secretion, which is always under pressure. It is longer than the efferent duct.

(v.) No valve is required at the mouth of the afferent duct into the chamber; nor are there any muscles to open it. Its opening and closing are automatic.

The Mechanism of Suction.

The functions of the different parts concerned in suction have now been described under their respective headings. The present section gives a connected account of the mechanism, summarising, at the same time, what has been said above. The following is a picture of the mechanism as it might be imagined from the arrangement of the different structures described.

The mechanism consists of many structures in the dead coordinated with one another, from the piercing of the epidermis of a leaf by the stylets to the digestion of the sap in the stomach.

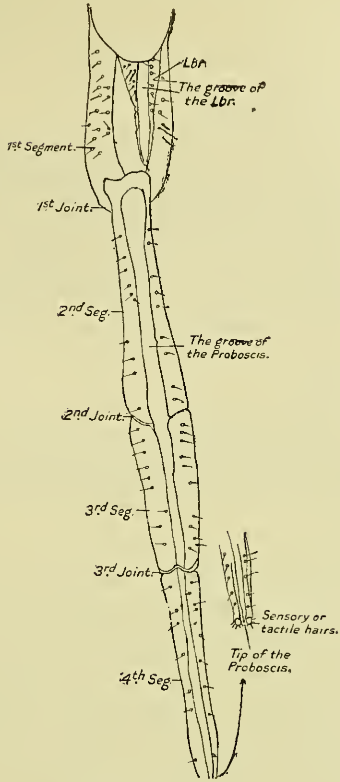
(1) The stylets inside a leaf.

The insect begins to feel the surface of a leaf with the sensory hairs at the tip of the proboscis (text-fig. 29). It is trying to find a good place for piercing. When it is found, the proboscis is applied to it, the stylets are driven forward, the protractors contract, and the epidermal layer is pierced, however thick it may be.

(2) The bending of the proboscis.

Once in, the stylets are pushed down into the tissue by direct mechanical force, *i.e.* by the bending of the proboscis. This feature has already been alluded to. It increases artificially the protrusion of the stylets and enables them to reach the tissue which contains food. It seems that the insect is not confined to any particular plant-tissues. The stylets may be found in the xylem, the phloem, or in the cortex which contains food-substances (text-figs. 24, 25).

Text-figure 29.



Lygus pabulinus.

Mount, showing the labium macerated in potash and stained with saturated picricin, 90 per cent. alc.

(3) Injection of Saliva into the wound.

When the stylets reach the particular tissues, the maxillo-mandibular muscles begin to act. Their function has already been dealt with. The mandibles, when they are pulled in by these muscles, get fixed into the cellular walls by means of their recurved hooks (text-fig. 25). The maxillary stylets are made steady in their action by the mandibles because of their interlocking arrangement.

Before the sap is sucked through the suction-canal, it seems that saliva is injected into the wound made by the stylets. It is possible that the saliva, by being mixed with the sap, may trans-form starch into sugar and thus help its digestion. Plateau (41) has proved that the saliva of insects has this effect. It is doubtful whether the sap is coagulated by exposure to air, but if so, the saliva may prevent its coagulation. A third possibility is that saliva may make the sap less viscid.

(4) Turgidity of the Cells.

This may be important indirectly in forcing the sap mixed with saliva into the suction-canal of the maxillary stylets. The cells of a tissue are always turgid and their walls are stretched to their utmost capacity. They collapse if pricked, and squirt out the sap with some force. The maxillary stylets pierce the cells, the sap of which may thus be forced into the empty suction-canal, since the other canal is full of the salivary secretion. I attach no great weight to this possible factor in suction.

(5) Capillarity.

This factor may now come into action, and by its means the sap would begin to ascend in the suction-canal if this were open at the top. The sap reaches the pharyngeal duct, which hangs into the suction-canal, and is thus immersed in the sap.

(6) Suction.

The divaricators of the pharynx begin to act. Those of the anterior part of the clypeus contract first. The operculum is pulled out and a vacuum is formed between it and the "V." The sap is sucked into the pharynx from the pharyngeal duct. The muscles relax, and the operculum regains its former position. Meanwhile the muscles lying posteriorly contract, the operculum is pulled out, and the sap is forced onwards. The muscles lying still more posteriorly, do the same thing, and the same process is repeated. Thus there is a wave of contraction of muscles passing backwards, and the sap is continuously forced on towards the stomach. It is prevented from flowing back, because there is no empty space behind, since the operculum regains its normal position with relaxation of the anterior muscles.

Thus, in the pharynx there are two complementary factors which force the sap onwards towards the œsophagus :—

(i.) The vacuum produced by the raising of the operculum.
(ii.) Elasticity of the operculum, which enables it to regain its normal position.

(7) The Œsophagus.

The sap is forced into the œsophagus, the walls of which are soft and flexible and have attached to them the constrictor muscles. As the sap distends the walls, the muscles contract, and a peristalsis is produced which forces the sap onwards towards the cardiac valve.

(8) The Cardiac Valve.

The valvular muscles contract, the valve opens, and the sap is forced into the stomach.

(9) The Stomach.

This is a bag-like structure and stores the sap.

To sum up :—

There are the following factors at work :—

(i.) Capillarity in the suction-canal, helped by turgidity of the cells.

(ii.) Suction produced by the vacuum through the raising of the operculum.

(iii.) The peristalsis in the œsophagus by means of the constrictors.

(iv.) The valvular action, which prevents the sap from flowing back into the œsophagus from the stomach.

The pharyngeal duct hangs into the suction-canal and is immersed in the sap. A question arises whether it is possible for the sap to avoid the duct and flow into the body-cavity from the suction-canal. The sap cannot do so because (i.) there is no difference of pressure to force the sap into the body-cavity, and because (ii.) there is active suction through the pharyngeal duct.

Another important thing for suction is that the suction- and ejection-canals must be separate and distinct from each other. The least intercommunication will stop the whole mechanism. Also one canal cannot serve two contradictory purposes—one of sucking and the other of ejecting saliva. The whole mechanism, therefore, depends upon the presence of the two canals. (But, curiously enough, the Bed-bug, *Cimex*, is stated to present such an anomalous case. It has only one canal for sucking the blood and ejecting the saliva as well. Recently it has been described by Dr. Max Braun (**1**): "In shape the maxillæ resemble two gutters, the concave surfaces of which face one another and so form a tube. This serves to conduct the blood from the wound into the pharynx and also saliva into the wound. In other Hemiptera food and saliva are conveyed by two distinct channels formed by the longitudinal ridge which runs down the groove of each maxilla, dividing it into two parts." This is not the case actually, as I hope shortly to show by figuring sections of its mouth-parts.)

Damage to the Plant.

That *Lygus pabulinus* does some damage to potato plants has been conclusively proved by the elaborate experiments of Prof. Lefroy, of the Imperial College of Science, and Mr. Horne.

It is sufficient to say here that the insect drills into the leaves holes which are bordered afterwards by brown rims. It does not come within the scope of this paper to deal with the pathological effects due to the insect-bites; but the way in which these holes are drilled is described below.

The structure and the shape of the stylets have been described above. The tips of the maxillary stylets are smooth and lancet-shaped, but those of the mandibles are deeply serrated (text-fig. 23). The tip of the proboscis is covered with stiff hairs and is blunt. How the stylets work inside the plant-tissue has been described above. The insect is found on the same place for hours at a stretch. It withdraws its stylets every few minutes from the plant-tissues and thrusts them in again. This process is repeated many times. Since the mandibles can only be withdrawn by tearing the cells each time they are taken out with their recurved hooks (text-fig. 25), and as this process is repeated many times, a big area is ultimately macerated and a hole is formed there afterwards.

It was held by many writers—Dr. Riley being one of them—that the Heteroptera made holes with the proboscis, the Homoptera with the stylets. This view is absolutely inaccurate, since it is found that the proboscis is incapable of drilling holes, its tip being too thick and blunt to pierce the epidermis. Sections of plants taken with the stylets *in situ* show that the stylets enter the tissues, the proboscis itself remaining outside, as described above.

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